THE ANOLES (SAURIA, IGUANIDAE) OF THE LESSER ANTILLES

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CONTENTS

FOREWORD

This work goes to print somewhat modified from the doctoral dissertation submitted to the University of Rhode Island in May, 1968. The principal modifications have been deletions. Originally written as "the iguanid lizards of the Lesser Antilles," the entire section on *Iguana*—the only other living genus—has been removed and will be published elsewhere. A scathing critique of mathematical approaches to island biogeography has been cut, simply because my emotional involvement against that nefarious pseudoscience precluded a report that was not vindictive and vitriolic.

Most important to me, what now follows seems dry, dull, and stultifying. I tried not to write it that way, for I firmly believe that unless scientists can make their work interesting, or even entertaining, it will not be read, even by their colleagues and fellow specialists. As I read over these pages now, I find scant allusion to what it was like to spend a decade—in the field and in the lab—getting to know this remarkable fauna. Gone from these pages are the perils of caclin bush and huge vipers; nothing remains of giant boas and Cicero parrots; there is no more the taste of salt and blood on the rocks in the surf at Pelikan Cay or Kick-'em-Jenny. Counting subdigital lamellae, or arguing over the best possible species definition, is dull work indeed. Sadly, that is about all that now remains.

It has been over two years since the last revision of this work was done for the University of Rhode Island. I have long moved on to a study of the herpetology and ecology of our coastal islands from Cape Cod to Cape Fear, and have not now time to rewrite this as I did the original. Publi-

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[1] Massachusetts Audubon Society, Lincoln, Mass. 01773.

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cation of this work is overdue, in any form, and these are hard times: the cost of a printed page is high indeed. So, to make up for all that what follows lacks, I recommend to you the Lesser Antilles: the sea, the islands, the people, and, of course, the iguanid lizards. In reality, they are very far from dull.

James D. Lazell, Jr.

ABSTRACT. The iguanid lizards of the genus *Anolis* from all islands from the St. Croix Bank southward to the Grenada Bank are reviewed systematically. Two major groups are recognized; the *bimaculatus* group, from the northern islands (St. Croix to Dominica), has three parasternal chevrons attached to dorsal ribs; the *roquet* group, from the southern islands (Martinique to Grenada), has four chevrons attached to ribs.

Nine species of *bimaculatus* group *Anolis* are recognized: *acutus*, *wattsi* (with four subspecies: *wattsi*, *forresti*, and two newly described), *sabanus*, *gingivinus*, *bimaculatus* (with two subspecies: *bimaculatus* and *leachi*), *nubilus*, *lividus*, *marmoratus* (with twelve subspecies: *marmoratus*, *alliaceus*, *girafus*, *setosus*, *kahouannensis*, *speciosus*, *inornatus*, *desiradei*, *chrysops*, *ferreus*, *terraealtae* and *caryae*), and *oculatus* (with four subspecies: *oculatus*, *cabritensis*, *montanus*, and *winstoni*). Morphological, karyotypic, and geographic considerations lead to an opinion that *Anolis acutus* is the primitive member of this group, and that evolution has been in some five stages of radiation; the most recently evolved full species is thought to be *Anolis nubilus*.

The *roquet* group is divided into seven species: *luciae*, *griseus*, *richardi*, *trinitatis*, *aeneus*, *extremus*, and *roquet* (the latter divided into five subspecies: *roquet*, and four newly described). Morphological, karyotypic, and behavioral evidence argues strongly that *Anolis luciae* is the most primitive member of this group, and that *Anolis roquet*, and its subspecies on Martinique, is the most recently evolved. Five stages of invasion and differentiation are envisioned for this group, too.

The theory of species group level taxonomy on oceanic islands is given especial consideration; it is suggested that the "biological" species concept is neither logically nor theoretically applicable in many cases, and that the inclusive evolutionary species concept of Simpson (1961) is required. The geology and climatology of the Lesser Antilles are discussed in detail, and reconstructions of the evolution of the lizards are developed in that context.

THE LESSER ANTILLES: AN INTRODUCTION

> In no other regime on earth do the winds blow so steadily. Life has adjusted to this uniform wind stream in numerous ways.
>
> —Herbert Riehl (1954)

The basin of the Caribbean is the great cul-de-sac of the western North Atlantic. Separated in the north from the Gulf of Mexico by Yucatan and the Greater Antilles, this sea is bounded on the west and south by solid land long known simply as the "Spanish Main," but today composed of the Mexican State of Quintana Roo, the Crown Colony of British Honduras, and the Republics of Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Venezuela. The equatorial surface waters of the Atlantic are swept unceasingly into the Caribbean cul-de-sac; to quote Slocum (1900): "the trade winds . . . , produce this current which, in its course . . . , is governed by the coastline of Brazil, Guiana, Venezuela, and, as some would say, by the Monroe Doctrine." This great current of surface water, pouring into the Caribbean cul-de-sac from the southeast, must change direction to get out again in the northeast: it is strained between Cuba and Yucatan into the Gulf of Mexico, fended off by the vast, shallow banks of the Bahamas, and sent ripping through the Straits of Florida to form the Gulf Stream.

The Trade Winds are best regarded as a vector quantity; air, heated in the equatorial area, rises to great elevations, cools, and descends towards the temperate latitudes of the earth; pushing back across the surface, it completes its cycle. At the surface of the earth, convection currents provide a north-to-south Trade Wind component in the northern hemisphere, and an opposite, south-to-north Trade Wind component in the southern hemisphere. The residual inertia of the air mass surrounding a rotating earth provides a continuous east-to-west Trade Wind component. Thus, surface water in the southern Atlantic is literally blown northwestward against the continental mass of South America, whence it is swept into the Caribbean. The Trade Winds themselves sweep into the Caribbean basin from the north and east, unimpeded by any continental barrier.

This simple picture has but one major complication: the earth is tilted on its axis. As the earth orbits the sun, the shortest distance from earth to sun is caused to move from the equator northward and southward, producing the alternating pattern we call seasons. The effects of the seasons are different in tropical regions such as the Caribbean than they are in temperate climes; the sun is always comparatively close, and temperature variations at the earth's surface are therefore comparatively minor. The small fluctuations that do occur, however, may be antecedent to storms whose violence and destructive potential are unmatched by other phenomena of man or nature.

When the shortest distance from the earth to the sun has reached its northernmost limit, the Tropic of Cancer, the summer solstice is reached; as the earth orbits, the shortest distance from the earth to the sun again coincides with the equator, and the autumnal equinox has been attained. From about the summer solstice until after the autumnal equinox the tropical North Atlantic is slightly warmer, on the average, than is the tropical South Atlantic; the northern equatorial air mass is usually somewhat warmer in correspondence, and the upward beginning of the convection currents is, as a result, comparatively strong. Cooler, southern air may sometimes be pushed by the Trade Winds across the equator. The resulting clash of temperatures and pressures can create a sudden "bulge" of rising, warm air in a local field of descending, cool air; this bulge, with its concomitant suction of updraft, may, under the influence of Coriolis effect, begin to swirl: a cyclonic storm may be born. This beginning may occur anywhere in the north equatorial Atlantic from Africa to the Caribbean. Often, there is a tendency for these cyclonic storms to be carried westward by the wind and current; they may be swept into the basin of the Caribbean and, gaining tremendous velocity of rotation, become West Indian Hurricanes. For sheer force, the West Indian Hurricane may be compared only to its sister storm, the Pacific Typhoon.

Across the mouth of the Caribbean cul-de-sac extends an arc of small massifs. Rising independently from the bottom of the sea, these massifs form submarine banks which, in most cases, are today topped by islands: The Lesser Antilles. These islands rake the air and sea pouring into the Caribbean cul-de-sac like the teeth of a gigantic comb. Hurricanes, when their paths are averaged, may show a tendency to approximate the current flow and leave the cul-de-sac in the north and east; but individually they are often deflected southward by the push of the Trade Winds, and the comb of the Lesser Antilles may thus strain out detritus borne across the sea from the west and north. No method for accurately predicting the path of any hurricane has ever been devised.

The Lesser Antilles are truly oceanic islands. Although cycles of glaciation have caused sea level fluctuations probably uniting most of the islands on a given Lesser Antillean submarine bank (see Flint, 1957: 258–271), there is no evidence that any connection has occurred between islands on different banks or from any Lesser Antillean bank to any other land area. Matthew (1915, 1918, and 1930) progressively built the case against continental connections to the Antilles until it was unassailable. The entire polemic and the views of Matthew's principal antagonist, Thomas Barbour, are available under one cover (Matthew, 1939).

The causal zoogeography of oceanic islands, such as the Lesser Antilles, is simplicity itself. Aside from the recent introductions of man (which have had but scant effect on Lesser Antillean iguanid lizards), the land animals of the Lesser Antilles are descendants of what Dunn (1934) aptly called "waifs"; these usually reached the islands by passive "waif dispersal" across the sea rather than by any active intentions of their own. There can be no genuinely predictable patterns of land animal distribution on oceanic islands. Land animal distribution here has been controlled by two major factors: the whimsy of the wind, and the caprice of the sea.

Davis (1926) provided the most detailed account of the physiography of the islands and their geological composition. Following this, two principal subdivisions may be recognized:

The *first cycle islands* form a continuous inner (western) chain, beginning with Saba in the northwest and extending to the southernmost cay, Glover Island on the Grenada Bank. These islands are of igneous, extrusive strata, and many are still actively volcanic.

The *second cycle islands,* beginning at the extreme northern end of the arc with Sombrero, and extending southward only as far as Marie Galante, are older; their igneous strata are largely eroded away, and they have been submerged and capped over with oceanic limestone, a sedimentary stratum. Many of them still have old basalt spires protruding from the limestone, but all are low in elevation (under 1400 feet).

Barbados lies on a continental base. On the same ridge as Tobago, Trinidad, and the Coastal Andes, this island has, like those of the second cycle, been submerged and capped with limestone.

St. Croix also resembles the islands of the second cycle, though its base (and protruding highest hills) are of sedimentary rocks: slates and shales. Although St. Croix is distinct from the eroded plutonic rock islands of the Puerto Rico Bank, including all the other Virgin Islands, it is distinct from its Lesser Antillean neighbors also in not being of volcanic origin.

The tiny atoll of *Aves* lies far at sea, west of Dominica and south of Saba. It lacks iguanid lizards, and need not concern us here (see Lazell, 1967a). The banks and major islands are shown in Figure 1.

The only historical geology of these islands is that of Schuchert (1935). Schuchert was a bridge-builder; he erected land bridges across wide areas to explain the presence of a single form on a particular island. The distribution of animal life in the Lesser Antilles fails to support any such hypothetical land bridges, either between the Lesser Antillean banks, or from them to either the Greater Antilles or South America.

Two major meteorological generalizations are evident in the Lesser Antilles: (1) the wind blows from the northeast, (2) clouds (cumulus) lie at 2000 feet.

The first of these, wind direction, is subject to change only at times of imminent storm: the hurricane season from June to November. In this period the wind may shift temporarily from its usual direction.

The second generalization, that clouds lie at 2000 feet, is subject to greater inaccuracies. As a generalization, however, it is excellent. I kept notes on the lower limit of cloud line on La Guadeloupe for six weeks in August and September of 1961; never did the cloud line lie below 650 meters, and there were always at least some clouds at 700 meters along the mountain range. (The 2000-foot line is between these two elevations.) In nine years of collecting in these islands, from three to four months per year, I never saw cloud lines below 1300 feet, and some clouds (even on the clearest days) were always present below 3000 feet. The only cloud formations of immediate concern are those which bring rain: cumulus and strato-cumulus. Cumulus is produced directly by evaporation off the tropical Atlantic, and strato-cumulus results from cumulus backing up against a mountain range and

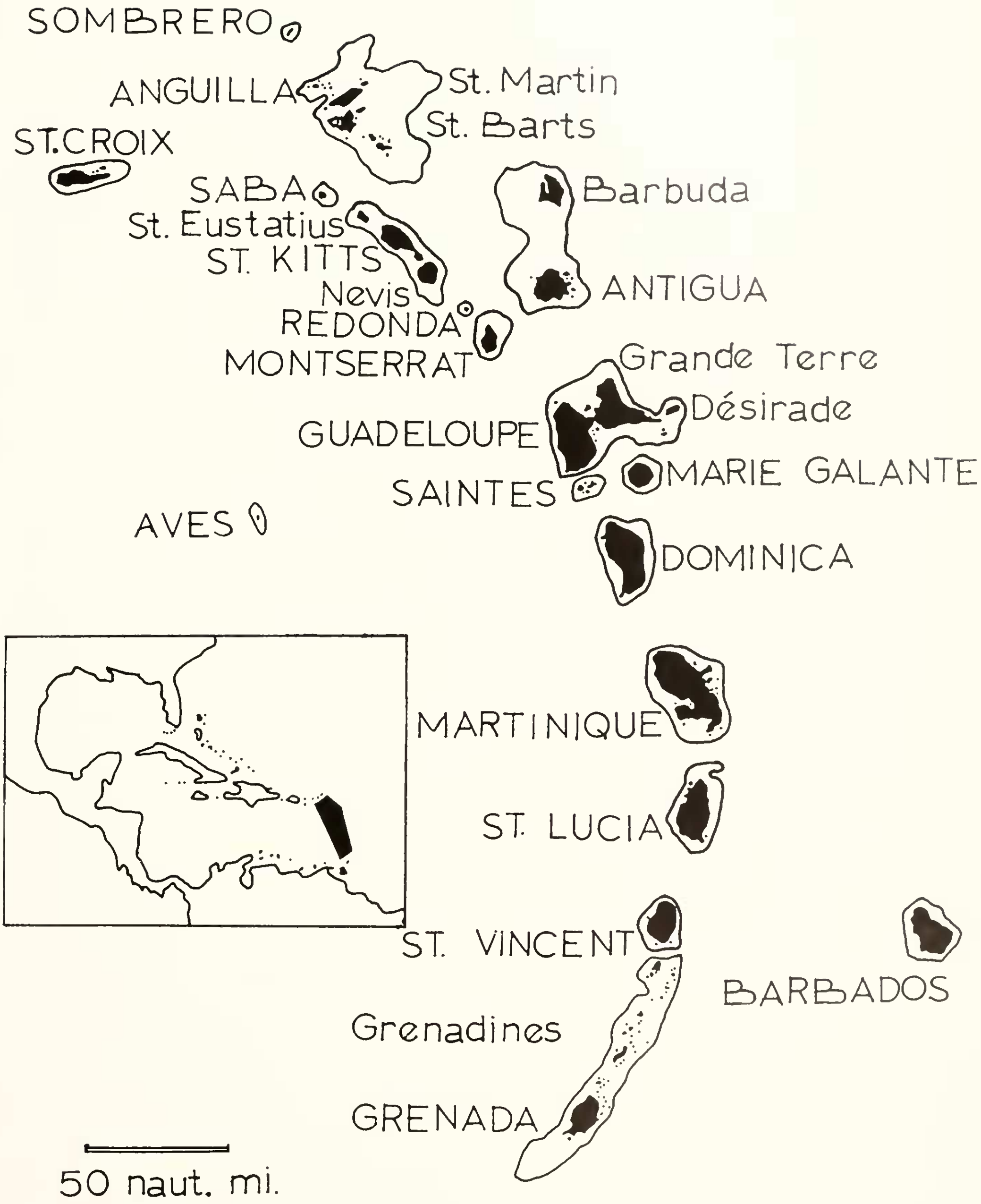

Figure 1. The Lesser Antilles. Approximate bank borders are indicated; banks are named for their largest island (capitalized). The inset shows the position of the Lesser Antilles (black) relative to the other land areas of the Caribbean Basin. (From various sources.)

Figure 2. The three kinds of first cycle islands that affect precipitation by their land forms, and the general pattern of cloud cover they induce (hatching). Compass direction is indicated lower left, wind direction upper right. See text.

combining with water evaporated from the land and vegetation.

The second cycle islands, Barbados and St. Croix, are nowhere sufficiently high to stop or hold any quantity of clouds. With the single exception of southwestern Grande Terre, which lies close enough to windward of La Guadeloupe to be well watered lowland, all of these islands are dry. They receive 35–75 inches of rain, on the average, per year. The open ocean receives 35–45 inches. Rainfall data for these areas may be found in U. S. Navy Hydrographic Office Publication 22 (1963).

Some first cycle islands are sufficiently high in elevation to receive great quantities of rain. On the northern leeward coast of Dominica, rainfall averages about 45 inches per year; six miles inland, amid peaks rising to nearly 5000 feet, from 350 to 450 inches of rain fall per year (Beard, 1949; Hodge, 1954). The spectacular differences between localities separated by short distances in the first cycle islands, and their implications for the flora, have been discussed by the authors cited immediately above, as well as by Stehle in numerous papers (see especially 1936), and Stoffers (1956). Lazell (1962, 1964a) discussed the implications of these changes for some elements of the fauna.

Thus the initial, and major, causal factor in rendering land areas wet or dry is elevation. Beard (1949: 15) has mistaken the secondary causal effects—those which result in wet lowlands—as proximity of the mountains to the coast. As is evident from Lazell (1964a), Stehle (1936), and reason, the height and spacing of the mountain peaks is far more important in producing wet lowlands than is their relative distance from the coast.

To clarify this, Figure 2 shows the three sorts of mountain arrangements possible in these islands.

"*Snag*" islands have a single high peak (over 2000 feet) that catches a small bit of cloud and is able to hold it, largely through evaporation from the island; their lowlands are quite dry. Such islands are Saba, St. Eustatius, and Nevis.

"*Overspill*" islands have two or more high peaks, or massifs, that are either too low or too separated to effectively halt the clouds in their southwestward traverse, and therefore, for the most part, only slow them down. In these cases the clouds are usually strung out to leeward of the mountains; the leeward coast may be as wet as the windward coast, or even wetter. Examples of "overspill" islands are St. Kitts, Montserrat, St. Lucia, St. Vincent, and Grenada.

"*Barrier*" islands are those on which the mountains are sufficiently high and close enough together so that they effectively stop the clouds. Clouds, therefore, pile up to windward, forming a wet region for some distance, and rarely overlie the leeward coastal areas, which are, therefore, exceedingly dry. The leeward slopes of barrier island mountains are clothed in rain forest to as low as 2000 feet; then an abrupt shift to arid lowlands occurs. This is explained by the fact that precipitation is "whipped over" the peaks from the windward, as described by Geiger (1959). Examples of "barrier" islands are La Guadeloupe, Dominica, and Martinique, the largest and highest islands of the arc.

Of the banks of islands in the first cycle, only two, Redonda and Les Iles des Saintes (both tiny), are too low to have rain forest or montane plant associations. All three islands on the St. Kitts bank have them (all of these islands are small in comparison with La Guadeloupe, Dominica, or Martinique). Each of the remaining banks contains a single island with rain forest. The three largest islands, La Guadeloupe, Dominica, and Martinique, have by far the most extensive rain forest areas and the greatest complexities of montane plant associations in the Lesser Antilles.

In attempting a synthesis of ecological information, the political diversity of the islands has been a handicap. Stoffers (1956) is my sole reference to land plant ecology in the Dutch Islands. The French Islands are perhaps the best known of the entire chain. For information on general distribution, zonation, and succession, Stehle (1936, 1937a, 1937b, and 1941) provides accounts as detailed as could be desired. Stehle's (1945–46) attempt at a synthesis of plant ecology for all the Caribbean islands is poor, owing to his lack of information on those islands not part of France; the map provided there is, however, very useful in ascertaining the general distribution of floral ecological zones.

Dominica has been treated exhaustively with respect to floral zonation and succession by Hodge (1943, 1954), and taxonomically by the Conservator of Forests, Trinidad and Tobago (1944), and Beard (1949). All of the islands south of Martinique are British, and the two latter references have supplied the bulk of my information on them, augmented by Sands (1912), for ecological succession, and Grisebach (1864).

I use the general term "rain forest" to combine both "lower rain forest" and "montane rain forest" (*sensu stricto*) with the three montane formations represented —montane thicket, palm brake, and elfin woodland—all *sensu* Beard (1949). In Saba and St. Eustatius the very depauperate and tiny areas of "rain forest" are an admixture of all the types mentioned above except lower rain forest. In St. Kitts, Nevis, and Montserrat the floras are richer and zonation more apparent; lower rain forest is, however, absent from these islands, too. St. Lucia, St. Vincent, and Grenada have small areas of lower rain forest; St. Vincent, however, apparently lacks elfin woodland.

Only the "barrier" islands, La Guadeloupe, Dominica, and Martinique, have all five associations well developed. In these islands the highest peaks are often covered by *Clusia mangle*, referred to as "*caclin*"; this nearly impenetrable tangle of large trunks may form a continuous covering over exceedingly broken terrain, and is often deceptively dangerous to travel through. It might be best regarded as a separate consociation, rather than as a type of elfin woodland.

Exhaustive information has been available for the typical "overspill" island of Grenada. This includes Knight (1960), G. W. Smith (1961), and the manuscripts of Cromwell (1960a, 1960b, 1961); the clearest and most detailed pictures of ecology on an "overspill" island may be seen in Regional Research Centre of the British Caribbean Publication 9 (1959). The complex integration and blending of rainfall distributions, land humidity, and topographic relief distort ecological zonation on "overspill" islands far beyond the relatively simple picture presented by Hodge (1943,

1954) for Dominica, a typical barrier island.

The island of Martinique, largest in the chain, is the most complex. It forms a typical barrier in the north, but overspills and has snags in the central and southern regions; the extreme eastern end of the Presqu'île de la Caravelle and most of the southeast extremity, Pointe des Salines, are so far removed from the rest of the land mass, and so low in elevation, as to be climatically similar to second cycle islands: arid and xeric. Stehle (1937b, 1941) has discussed this complexity from a floral viewpoint, and I will here give it further consideration under *Anolis roquet.*

King (1962), after an excellent discussion of waif dispersal (pp. 38–40) is guilty of an over-generalization: that propagules should be expected to infiltrate the Lesser Antilles along the course of the averaged storm tracks: "If the lizards are dispersing southward in the Lesser Antilles, they are being carried against the ocean currents, against the prevailing winds, and against the direction taken by cyclonic storms" (p. 40). He concludes that for the geckos of the genus *Sphaerodactylus,* at least, it is far more likely that they have come north and west, from South America. It seems clear, however, that the nine species of *bimaculatus* group *Anolis* must have come south and east from the Greater Antilles (see below). The writer agrees with Darlington (1938) that windstorms are of major importance in transporting small lizards, like *Anolis.* The answer to this apparent dilemma is in avoiding a generality about storm tracks: averaging storm tracks in the Caribbean is no more valid or useful than averaging the direction of long distance 'phone calls leaving Boston; it tells us nothing about the direction of a particular storm (or 'phone call) in the past, and provides no predictive information about the direction of any future storm (or 'phone call) that does not absolutely require to be checked by empirical observation. U. S. Navy Hydrographic Office Publication 22 (1963) gives speed and directional data for tropical storms and hurricanes in the eastern Caribbean region; especial attention is called to figure 15 (p. 49) of that volume, which shows an individual storm proceeding directly from the eastern Greater Antilles into the northern Lesser Antilles at 16 knots, as well as numerous other storms not going in the average direction.

Tannehill (1952), the authority on the subject of hurricanes, sums up (p. 55): "Much has been written about average storm tracks but they are of little value. . . . While a large percentage of these tracks are described as 'parabolic,' there are numerous exceptions." Average storm tracks have no place in serious zoogeography.

Underwood (1962) provided a historical essay on reptilian systematics of the Lesser Antilles; he stated of Linnaeus (p. 7) that "he probably did not have any specimens from any of the islands and presumably knew nothing of their fauna." That is not quite true: Linnaeus (1758) described the largest known Lesser Antillean snake, *Constrictor c. orophias* (see Lazell, 1964b), although he did not know where it had been collected. Also, he described the largest lizard, *Iguana iguana,* although he knew merely that his specimen came from "the Indies." With that correction, the nomenclatural history of Lesser Antillean iguanid lizards may stand as amply reviewed by Underwood (1959, 1962).

The Lesser Antilles are a fascinating chain of islands; to quote Vandercook (1938), perhaps their most sympathetic chronicler, "within sail, and often within sight, of each other are the colonies and cultures of more nations than one may find . . . so close together anywhere else on earth. . . . Nowhere else is so much variety so accessible." He also notes: "Men of all nations drifted to the islands." I did myself. "They found peril, strangeness and beauty—all they had come for."

MATERIALS, METHODS, TERMS, AND CONCEPTS

> 'When I use a word,' Humpty replied, in a scornful tone, 'it means just what I choose it to mean—nothing more nor less.' 'The question is,' said Alice, 'whether you can make a word mean so many different things.' 'The question is,' said Humpty, 'who is to be master, that's all.'
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> —Lewis Carroll (1866)

The present revision is based on the examination of about 10,000 specimens in the following institutions: Museum of Comparative Zoology (MCZ), Muséum National d'Histoire Naturelle, Paris (MNHN) Albert Schwartz Field Series (ASFS); and my own collection (JDL).* Of these specimens, I collected about 8,000 between June, 1958 and April, 1966. With the exception of a few collected in 1958, all specimens collected were carefully annotated in life with respect to coloration, habits, habitat, and general behavior. Field sketches, in color, augment the catalogued notes. My field catalogues contain information on the lizards, snakes, frogs, and other animals of the islands, as well as observations on their plant life, topography, climate, and people. The information relevant to particular species or places is available on request.

COLLECTING

The best general description of herpetological collecting technique is that of Mayer (1967); the methodology there depicted corresponds to that frequently used with Lesser Antillean iguanid lizards, though some sophistications have proved valuable. In general, lizards are best caught with a noose. This method does not normally damage the specimen in any way, and delivers it live into the collector's hand. I prefer, for *Anolis* and lizards of similar size, a monofilament (fishing leader) noose extending from the tip of a fiberglass, three-piece fishing pole. I prepare the noose as follows: tie monofilament of 6- to 15-pounds test weight in a hard square knot on a wooden match stick; break the match stick at the point of the knot, thus freeing the monofilament; cut off the monofilament about 18 inches from the knot (and its now-present, small loop—previously encircling the match stick), and pass the cut end through the small loop; masking-tape the monofilament to the pole tip about one inch from the noose now formed, after closing the noose to a suitable size; spiral the monofilament down the pole and tape it again; tying it to the pole after the second taping is a good idea. A noose carefully made in this manner may catch 300 lizards. Catching a lizard is simplicity itself: place noose around lizard's neck and pull. Anybody can catch a lizard, and in the West Indies, at one time in life or another, almost everybody does. It is catching the particular lizard you want that may be difficult. High up on a sodden, windy peak, with a thunderstorm visibly and rapidly approaching to windward, a magnificent specimen of some montane rain forest form, squirrelling farther and farther out on the caclin trunks over a great abyss, can lead to intemperance in a man. I have shot my share of lizards.

Locality Data

I have tried to keep my locality data on specimens as vernacular as is consistent with some readily available map. Translating the English place names used on Saba, St. Eustatius, or St. Martin into Dutch, merely because the islands belong to the Netherlands, is sheer affectation; no one there speaks Dutch under normal circumstances. The Lesser Antilles boast a plethora of Mornes Rouges, Marigots, St. John's, and Green Islands; whenever collecting at one of these localities I have been careful to specify which, even if I had to improve on the map in so doing. Thus, "Morne Rouge (du Nord), La Guadeloupe" delimits which of the two places on the island

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* Now all deposited in the MCZ.

is meant, even though the parenthetic statement is my own addition. Small islands tend to have simple, rather charming place names: it might be uncomfortable to spend a night on sandy ground, but at Sandy Ground (Anguilla) things aren't so bad. You can easily go from The Level to The Bottom (on Saba), and Behind the Mountain is precise, not relative (on St. Eustatius). Malendure (La Guadeloupe) and Porte d'Enfer (Grande Terre) speak for themselves. A number of the Grenadines have already become well known in ornithology as great nesting cays: the Battowi' Bullet, All-a-Wash, and Kick-'em-Jenny. The spelling of other Grenadine names has been a problem for me. The terminal "a" in Bequia and Battowia is not pronounced, but all the maps retain it, so I have, too, in catalogue entries. Many of the cays have names now much modified from their original French: Ile-à-Quatre of some maps is just called "Cot" by people in the Grenadines; I have compromised at "Quatre." Petite Tobago is called "Patty Taback," and "Petite" is always called "Patty" there; I have retained French spellings for lack of a real alternative. In the case of the Ile-à-Ronde, the Ile-à-Caille, and some others, I have improved on the map; their mapped names are usually given as Isle Ronde or Isle-o-Ronde, but those are neither French, English, or the way the names are said: I have deemed Isle-a-Ronde, Isle-a-Caille, etc., as colloquially acceptable spellings, since they fulfill at least the last criterion. Many people deplore the use of St. Kitts for St. Christopher and St. Barts for St. Bartelemy, but those older, cumbersome, official names are simply colloquially incorrect: they are not even used on official documents. I may, perhaps, be taken to task at this point for insisting on La Guadeloupe for the island so often called "Basse Terre"; in this case, however, the official name is preferred because it eliminates confusion between the island (La Guadeloupe) and the capitol city (Basse Terre), and calling a spectacularly mountainous island "Basse Terre" strikes me as inappropriate.

Elevations and distances are given in the relevant local system: feet and miles on American and British islands, meters and kilometers on French and Dutch. I prefer the metric system, but consistency must here be sacrificed to sanity: giving elevations in meters for Dominica would hardly be useful; no map of the island uses them. For those not fully accustomed to thinking in both systems, this work may provide valuable practice.

The two best general maps of the Lesser Antilles are U. S. Navy Hydrographic Office (USNHO) 5487 and the National Geographic Society map of the West Indies issued in March, 1954 (and not to be confused with the abomination published by the same Society in December, 1962, as Atlas Plate 23). The Sombrero Bank is included in USNHO 1834, and the Aves Bank in USNHO 1011. For St. Croix I recommend U. S. Geological Survey MR 6849, 2445, and 5306. For the Anguilla Bank use the following: Directorate of Overseas Surveys (DOS) 343 (Series E848), Sheet 1 (Anguilla and Cays), Netherlands Antilles Cadastrial Survey Department (CSD) Topografische Kaart St. Maarten (St. Martin and Cays), and L'Institut Géographique National (IGN) No. 36, 1952 (St. Barts and Cays). For Saba the best map is CSD Topografische Kaart Saba. The St. Kitts Bank is excellently covered by CSD Topografische Kaart St. Eustatius, and DOS 343 (Series E848), Sheets 2 and 3, for St. Kitts and Nevis. For the remaining banks I list my preferences: Antigua Bank: U. S. Army Map Service E741 (Antigua and Cays), and the locally available British Survey Map (1848) of Barbuda; Montserrat Bank and Redonda Bank: DOS 359 (Series E803); Guadeloupe Bank, Marie Galante Bank, and Saintes Bank: IGN Guadeloupe (1958); Dominica Bank: DOS 451 (Series E703); Martinique Bank: IGN Martinique (1957); St. Lucia Bank: DOS

345 (Series E849); St. Vincent Bank: DOS 417 (Series E743); Grenada Bank: USNHO 1640, 1316, and DOS 342 (Series E844); Barbados Bank: DOS 418 (Series E749).

Preservation

Iguanid lizards should be fixed in strong (85–95 per cent) ethanol; methanol or isopropanol may be used as substitutes, but ethanol, in the common form of "cask rhum" is locally available almost everywhere. Formalin is very destructive to these specimens (Williams, 1962a: 455); I cannot repeat the facts too strongly: formalin usually alters the colors and patterns of these lizards to a dark, muddy condition unlike anything the animal was able to do itself; formaldehyde in solution (formalin) tends to go to formic acid (Lillie, 1954) and actually breaks down the epidermal (and other) structures: the scales become mealy and crumble away; bones decalcify and etch. The alcohols are far from perfect preservatives, and colors do, of course, fade; greens tend to become blue, reds tend to yellow, and yellow itself may completely disappear. The basic pattern, however, is usually very well preserved, at least in ethanol.

Specimens should be fixed in a flat tray, bodies straight, toes separated, tails brought parallel to the bodies. Specimens prepared in this manner are readily measured and examined.

Measurements and Meristics

The length of a lizard is measured from the tip of the snout to the anterior edge of the vent (= cloaca); it is vital to measure this length "over the curves" of the ventral surface: a straight line distance will be dependent on the position in which the animal was fixed.

Relative head width may be measured by numerous indices; I have used the distance across the supraorbitals at the narrowest point, as measured with vernier calipers, and divided this into the standard distance (see below). There are important differences and distinctions among many Lesser Antillean *Anolis* with respect to scale size; some method of quantifying scale size, therefore, requires codification. My preferred method has been the "standard distance count."

The standard distance is the straight line distance from the center of the eye to the tip of the snout. It is measured with vernier calipers accurate to a tenth of a millimeter. The accuracy of the calipers exceeds the possible accuracy of the measurer, for several reasons: the center of the eye (functionally, the center of the pupil) is in practice located visually, not quantitatively; the position of the animal's eye at time of fixation may affect the location of the center; the tip of the snout (premaxillaries) is clothed by layers of soft tissues, that, though shallow, may yield variably to the pressure of the caliper point at different times or for different measurers. Standard distance measurements and middorsal counts were made on several hundred specimens of *Anolis wattsi* in March and April, 1966. In August, 1966, I repeated measurements and counts on one hundred randomly selected individuals of this species without consulting previous data. When I compared the August data with the original, I found that my standard distance measurements were off as much as 0.2 mm (or about two per cent) in a few cases, but that every scale count was identical to that originally made. This is less remarkable, perhaps, than it seems, for *Anolis wattsi* have large, neatly aligned middorsal scales, and miscounts are hard to make. During June and July, 1966, I made counts of the middorsals contained in the standard distance at midbody on about 1,000 *Anolis marmoratus*. Most of these had been examined in 1962 and 1963, prior to publication of my work on the races of this species (Lazell, 1964a); some had been collected subsequently. While making the 1966 counts, I recounted dorsals contained in the standard distance on 200 specimens

Table 1. A table of shrinkage times and percentages for some Lesser Antillean *Anolis* specimens fixed and stored in ethanol. See text.

Species	Specimen	Date 1	Snout-vent (mm)	Date 2	Snout-vent (mm)	Time Lapse (Months)	Per Cent Shrinkage
OCULATUS	JDL 260	24.ii.66	90	3.vii.66	87	4	3.3
MARMORATUS	JDL 282	28.ii.66	85	13.vii.66	82	4.5	3.5
BIMACULATUS	JDL 230	15.ii.66	114	29.vi.66	110	4.5	3.5
GRISEUS	MCZ 82926	4.vi.64	135	1.vii.66	127	26	5.9
MARMORATUS	MCZ 71068	14.ix.61	80	1.viii.66	73	58.5	8.8
MARMORATUS	MZC 70769	11.ix.61	119	1.viii.66	102	58.5	15.5
BIMACULATUS	MCZ 75779	6.v.63	122	20.iii.65	113	22.5	7.4

included in the 1962–63 data (as well as on all fresh material). When I compared this new data to the original data, I found nowhere an error of more than five per cent; it must be remembered that dorsal scales are always much smaller than middorsals, and are not longitudinally aligned. I believe these examples demonstrate the repeatability of the method.

Of course, there are a large number of other methods for quantifying scale size that could be used. In the course of making standard distance counts on *Anolis richardi* and its close relative, *A. griseus*, I found a strong average difference: *A. griseus* had lower counts (= larger scales). When I calculated standard distance as per cent of snout-vent length, I discovered that *griseus* also had, on the average, a longer snout. What had seemed to be an average difference might be a sharp distinction, but for the proportional difference between the two forms. I therefore counted middorsals contained in ten per cent of the snout-vent length at midbody, and did find a distinction between the forms.

The scales of *Anolis,* in particular, are quite small, and may vary in size considerably on different parts of the body; around-the-body counts of *ca.* 250 may be obtained from species that are obviously distinct in various aspects of scale size: large middorsals may be combined with small ventrals in one species, the reverse true of another. Similarly, longitudinal counts will confound some forms with large nape scales and small middorsals with some other form that has large middorsals but undistinguished nape scales. It is, therefore, imperative that, whatever standard one uses, the distance in which scales are counted be short, or the quantification may be meaningless.

Shrinkage affects all preserved specimens. In Table 1 shrinkage is tabulated for a number of specimens that, because of their large size, were measured when fresh dead by the method of merely stretching them out on a page of my field catalogue and marking the positions of snout and vent; the distance between marks can then be measured anytime subsequently. Naturally, shrinkage will affect scale counts; I have not, however, had it do so to the extent that identification was compromised: even a 16 per cent shrinkage will affect a dorsal count a maximum of five scales, which will not put the average specimen outside the normal range of variation (Lazell, 1964a: 390). It is to be expected that if all fresh-dead, unpreserved specimens were used, the counts I give for fixed specimens would be consistently high: the head (and standard distance) presumably shrinks less than the body, owing to the relative rigidity of the skull.

Maturity

Sexual maturity is easily determined for female *Anolis* merely by the presence or absence of eggs in the oviducts; of course, some mature specimens may lack an egg, but it is certain that no immature specimen will have one. Male *Anolis* are more difficult to assess; in most *bimaculatus*-group species, the testes appear much larger in larger specimens and show clear internal development as a reticulate pattern on the surface: specimens with these features are regarded as mature. In some *roquet*-group *Anolis* (especially *A. griseus* and *A. richardi*) even the tiniest males may have large, reticulated testes: because all of these specimens have been fixed in such a way as to preclude good histological assays, I have, therefore, resorted to a subjective assessment based on the appearance of the testes, development of the hemipenes and throat fan, and general appearance of the individual.

Population

As the term is generally used (e. g., Slobodkin, 1963; Mayr, 1963; etc.) it is ambiguous. This ambiguity is useful and intentional. At its lowest level a population is what is called a "deme"—"the community of potentially interbreeding individuals at a given locality" (Mayr, 1963: 136); this is the panmictic unit. As well, a "population" may be used for a group of demes not taxonomically different from each other, like the population of *Bothrops lanceolatus* on Martinique. For the purpose of this paper, the term will never be used for a collection of more than one taxon. The term may thus mean anything from the deme to the species, but implies that all members of the population in question could interbreed, granted the obvious stipulations given by Mayr.

Form

This term is likewise intentionally ambiguous and is used, for example, by Smith and Taylor (1945) or Underwood and Williams (1959) to mean a taxon at the species group level: a species or a subspecies. Infrasubspecific assemblages (e. g., morphs, taxonomically indistinguishable populations, etc.) are not referred to as forms. Similarly, a "group" is a collection of similar, presumably closely related, forms, as used by the authors cited immediately above.

"Different" versus "Distinct"

All populations of West Indian reptiles exhibit *differences* from other populations. These differences may be minor, even statistically insignificant, or they may serve to distinguish all members of one population from all members of other populations. In the latter case, where no individuals of one population can be confused with individuals of other populations, the animals in question have reached that level of difference that constitutes being *distinct*. Populations that differ on averages, but where some individuals are equivocal in characteristics, are simply not distinct.

Similarity and Relationship

These two terms have caused great practical and philosophical difficulties in biology, but have virtually escaped notice as the causal agents of these difficulties by remaining etymologically buried in the vast poundage of printed matter that has accrued from essentially semantic arguments. Let us consider first of all "similarity." No organism (or anything else) possesses any similarity; a robin has eyes, wings, legs, feathers, haemoglobins, esterases, and so on, but it has no similarity. You can not weigh, measure, count, or in any other way quantify similarity. Similarity is an abstract, comparative concept that exists only in the mind of the observer (and, obviously, then only when the observer compares two or more objects or quantities). Mayr, Linsley, and Usinger (1953) go to great lengths to aid the systematist in quantifying "similarity," but they never succeed in this impossible task. What has been quantified are characteristics (real ones, that an organism actually has), and similarity has then been *inferred*.

Consider a hypothetical case involving three groups of organisms, A, B, and C. The members of each group possess a meristic character, N, which, let us say, is the number of scales between the nares. It is found by one investigator that the values for N are consistently A = 1, B = 4, and C = 5; the inference that B and C are more similar to each other than either is to A is immediate (with respect to the character N only, of course). Subsequently, however, another investigator discovers that A and C belong to a single, polymorphic species and that the counts of 1 and 5, respectively, for these morphs are controlled by a single pair of alleles, one of which displays complete dominance; there are no intermediates, all specimens of this species are either A morph or C morph. This same investigator discovers that B, on the other hand, is a distinct species, and that the count of 4 is polygenic in origin, and that the pleiotropic effects of the genes involved are of such great adaptive value that the character N (which counts as 4) is quite invariable. From the viewpoint of the second investigator, who considers quantity of genetic material involved, the loci of the genes, and the adaptive significance of N, the similarity of A and C (1 and 5) is vastly greater than that of either of them to B (4) with respect to character N.

The example is, of course, hypothetical and simplified. As a real example, is the dorsal stripe of a striped-morph California kingsnake (*Lampropeltis*) really "more similar" to the stripe of a ribbon snake (*Thamnophis*) than it is to blotches of its litter-mate kingsnake? A stripe is obviously more similar to stripe, one might say, than it is to a bunch of spots; but what if it is considered (still as a stripe) from a point of view other than color and position on the body? From the point of view of the genetic material that produced it, or its adaptive significance in the environment?

The point I have tried to make about "similarity" applies with equal force to that other abstract, comparative concept that also exists only in the mind of the observer: "relationship." This concept is even more difficult, however, because not even a systematic biologist can ever be quite certain just what it is that he means by it. Do we mean "propinquity of common ancestry?" If so, then the crocodilians must be regarded as more closely related to birds than they are to squamate reptiles: crocodilians and birds are the living members of the once great thecodont radiation, while squamates branched off the reptilian stock at an altogether different time and place; crocodilians and birds have a closer common ancestor, in time, than either has with the squamates. Propinquity of common ancestry is certainly a perfectly valid indication of relationship, but it does not cause us to group the crocodiles with the birds, and separate them from other reptiles. Is relationship "morphological similarity?" If so, then our placement of the crocodiles in the Reptilia appears justified, for we infer on the basis of many characteristics that crocodilians are more similar to other reptiles than they are to birds. We infer further that morphological similarities imply genetic similarities, and these also are a valid indication of relationship. In the future we may infer genetic similarities directly for many groups, but as yet we are able to do so only within a few small groups, such as the genus *Drosophila*, and then only partially. Ethology, physiology, and ecology also provide food for inference of relationship, but note that the phylogenetic taxonomist increasingly selects those sorts of relationship he regards as valuable, and discards others; no phylogenetic taxonomist, for example, allows himself to believe that the dietary correspondence of crocodilians to sharks implies a relevant propinquity of common ancestry or a relevant quantity of genetic material in common. This selection of characteristics, or, properly, narrowing of viewpoint, is the process of character "weighting." This process introduces a whole new dimension of subjectivity into phylogenetic taxonomy, and only further emphasizes the fact that similarity and relationship are assessments of the observer, not things with an objective reality of their own.

The relationships of taxa at higher categorical levels (above the species level) must always be inferred on the basis of similarity (or difference); there exist no other possible lines of evidence. This is, then, a process of compound inference: similarity is inferred on the basis of objective facts; relationship is inferred on the basis of similarity. It has been repeatedly shown, however, that in the categories species and subspecies (the only defined categories) the inferred similarities are not invariably a valid basis for the inference of relationship. (Examples relevant to Lesser Antillean iguanid lizards are cited in Lazell, 1964a.) This unfortunate fact leads directly to the problem of how we go about ranking indisputably real taxa in the categories of species and subspecies. As a solution to the problem, I recommend using definitions of the categories that are both practically applicable and theoretically sound.

Species

The definition here used is that of Simpson (1961): "An evolutionary species is a lineage (ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

The following assumptions are corollary to the concept of evolutionary species:

1. Evolutionary role is both expressed in and controlled by the characteristics of the organisms in question. That is, the characteristics of a population of organisms are to some extent a function of its evolutionary role, and its evolutionary role is to a complementary extent a function of its characteristics. This means that, while natural selection may alter the evolutionary role of a population (and thus alter its characteristics), the characteristics at any given time A directly specify the range of possibilities for natural selection to have modified by time B.

2. "Unity" is here taken to mean bound into an overall oneness—even if diversity exists within it—by progressive alterations in particular characters acted on by evolutionary processes, in such a way that continuity exists between the extremes of diversity, if the steps of a set of stairs may be said to exhibit continuity (they certainly may be said to exhibit unity).

3. Populations, but not individuals, may possess evolutionary roles.

The "biological" species concept of Mayr (e. g., 1942) is not applicable—either logically or practically—to the problem of classifying insular forms. It is certainly true that the finest possible evidence for evolutionary unity is interbreeding in nature; however, we cannot observe it, and it may not occur, between isolated, insular populations of the same species: other criteria must be used, and the concept of evolutionary role provides them (see *Subspecies*, below). Further, the fact that members of two separate species may, and sometimes do, interbreed and produce fertile offspring has one overwhelming taxonomic implication: neither actual nor potential interbreeding can be logically used as the sole criterion of conspecificity.

Subspecies

A subspecies is a population or group of populations occupying a part of the overall range of a species, that *combines diagnostic consistency with geographic continuity.* It is united to the other subspecies within the species in one of three ways: (1) actual intergradation (gene flow), (2) character clines through a series of isolated forms, or (3) tenable evidence that the differences between two isolates are the result of a founder effect in which one isolate appears to be directly derived from the other. (For details see Lazell, 1964a and, especially for geographically isolated forms, 1964b.) In many respects I agree with Wilson and Brown (1953): I do not recognize polytopic "subspecies" or subspecies in animals whose geographic variation is otherwise largely discordant; I do not recognize subspecies in cases where the zone of intergradation is large compared to the subspecies range (gradual clines); I do not recognize isolates that differ on averages, but are not distinct, as subspecies unless more than 75 per cent of the individuals involved can be identified correctly without recourse to locality data; finally, I do not consider distinct isolates to be subspecies of the same species unless it can be plausibly argued that they show a collectively unitary, or continuous, evolutionary role (i. e., comparative similarity is not sufficient evidence). Also, I do not consider a monotypic species to be a species with only one subspecies, but, rather, to be a species with no subspecies whatever: a subspecies is a special sort of geographical variant of which the monotypic species simply has no examples.

Many people take exception to these qualifications for subspecies. For example, Mayr (1963) defends polytopic "subspecies" on the grounds that they too have a geographic range. Polytopy is a case where animals having characters in common are not continuously distributed, but rather separated from each other by conspecific individuals that have different characters; so, however, are morphs, color phases, and the like. In reptiles, at least, it is usually easy to explain polytopy in terms of the independent development, in several separated populations of a species, of similar characters in response to some similar ecological condition; the resultant group of similar populations is convergent and polyphyletic with respect to the characters that they have in common. (For a discussion of what constitutes "monophyletic," as opposed to "polyphyletic," see Simpson, 1961.)

The subspecies concept is extremely useful in some cases of geographic variation, when large segments of a species conform in characteristics and geographic range. In other cases, however, the subspecific names may be far more confusing than useful. A great deal of geographic variation, some of it even spectacular in degree, simply does not produce the sort of pattern usefully regarded as subspeciation.

Sympatry, Dichopatry, and Parapatry

There are three possible geographic situations that may obtain between taxa: they may occur together in the same geographic area (sympatry), they may be separated from each other by a gap occupied by neither (dichopatry), or they may border on each other without either a gap or an overlap (parapatry). Examples of sympatry are obvious, and do not require recounting here. Similarly, dichopatric forms are common; e. g., forms confined respectively to islands separated by water inhabited by neither. Parapatric forms are exemplified by actually intergrading subspecies that abut along a zone of intergradation or hybrid belt; in some cases it is at least possible that full species may be parapatric, though usually only on a very temporary basis. In the use of these terms I follow H. M. Smith (1965), though "parapatric" was initially coined, as here defined, by Smith (1955). The adoption of the term "dichopatric" I regard as an unfortunate necessity. The older term, "allopatric," since it includes two very different biological situations, is no longer useful.

Clines

Strictly speaking, a cline is any sequential change in a condition or characteristic. In dealing with geographic variation in terrestrial vertebrates, it is useful to distinguish a variety of kinds of clines that may appear in the characters of the animals. When a given character changes sequentially in a particular direction over all or most of the geographic range of a taxon, it is regarded as a *gradual cline.* When the geographic area in which sequential change in a given character takes place is small compared to the areas in which no such sequential change takes place, the situation may be referred to as a *stepped cline.*

Previously (Lazell, 1964a) I used the term "stepped cline" for a situation where isolated, or dichopatric populations showed sequential change in one or more characters in such a way that the second population was intermediate in characters between the first and third, the third intermediate in characters between the second and fourth, and so on. This should properly be regarded as a *dichopatric stepped cline,* so as to differentiate it from the situation obtaining when two taxa abut along a stepped cline and animals of intermediate characters fill the gap. In the case of two taxa abutting along a stepped cline the biological situation is quite different (contact) than in the dichopatric stepped cline (no contact), and this situation should be referred to as a *parapatric stepped cline.*

Levins (1962, 1963) provides a very carefully worked out model for conditions that could lead to parapatric stepped clines without a blatantly ostensible ecological correspondence. Although the details of his model are too complex to discuss here (especially since no case of this seems to occur in the Lesser Antillean iguanids), they should be carefully considered when analyzing the etiology of stepped clines in, for example, widespread continental species.

Concordance and Discordance

As can be seen from the preceding comments, geographic variation of the stepped cline sort tends to produce a pattern where large areas of the animals' range show homogeneity of characters, and comparatively small areas show sequential change. Of course, it is possible that animals that display stepped clines in a number of different characters might have their clines so arranged geographically that the majority of the entire range was part of some cline or another. Such a case would be one of striking discordance in geographic variation, but (probably owing to the ecological basis of many stepped clines) I know of no such case in terrestrial vertebrates. When several stepped clines occur, they usually are more or less superimposed, or completely isolated from each other. Frequently, this pattern leaves large areas of homogeneity between the small border zones of sequential change, and permits the useful recognition of subspecies (providing the differences in characters are sufficiently great between animals in the areas of homogeneity).

Highton (1962) described just such a case of compounded stepped clines in the geographic variation of the North American salamander *Plethodon jordani.* Because he synonymized the subspecies in this case, one is left to assume that he regarded geographic variation in *P. jordani* as what he referred to as "nonconcordant"; the term "nonconcordant" does not appear in the English dictionaries available to me, but by tracing the stepped clines in each character onto transparent maps, and then superimposing the maps, one sees that the range of *P. jordani* is really divided into large areas occupied by diagnostically homogeneous populations, with rather narrow zones of sequential change, in one or sometimes several characters, between them. This pattern is concordant.

I can only interpret Highton's synonymization of the apparently well-defined subspecies of *P. jordani* as resting on a belief that "concordance" requires that every character change at every point that any changes. This is to say that every subspecies must differ from every other subspecies in every character that any subspecies differs from any other subspecies. Such a viewpoint is implicit, to some degree, in the argument advanced by Wilson and Brown (1953). Inger (1961), however, has pointed out the logical fallacy of such a viewpoint; to make this requirement strikes at the very heart of animal classification, for animals need to be, and in fact almost always are, classified as much on the basis of their characters in common with related animals as on the basis of their differences and distinctions from their relatives.

When more than one gradual cline occurs in the geographic variation of a species, and where one cline runs in a different direction from one or more others, discordance results. Edgren (1961) provides a magnificent example of just such a situation in the North American snake *Heterodon platyrhinos.* Examples of this may be fairly common, for the selection pressures resulting in gradual clines are clearly not very strong in any particular, confined portion of the species range, and ecologically based, weak selection pressures (like average temperature or humidity in the eastern United States) may themselves vary in ways directionally unrelated to each other.

In the cases of parapatric (actually intergrading) subspecies in the Lesser Antilles, the shift from one form to another is always clinal. It has been my policy to include within each subspecies only those populations in which I could find no intermediate individuals, or evidence of any intergradation. If I adopted the policy of Underwood and Williams (1959), and assigned populations to subspecies on "the balance of characters," the ranges of the various subspecies would be considerably larger and the zones of intergradation correspondingly narrower. Such a policy, however, compromises the integrity of what is, by intention, a presentation of the actual biological situation, and has not been followed.

Synonymies

The synonymies provided here are as complete as I can make them in the sense that I have located every available name I could, and cited it and its author; the references, of course, are cited in the bibliography at the end of the work. These synonymies are not "complete" in the classical sense that every usage of every name, and every combination of available names ever employed, is cited. Underwood (1959) and the lists of Barbour (1930a, 1930b, 1935, and 1937) will provide amusement for those intrigued by all the various combinations of names that are possible.

Keys

The keys given below have been idealistically conceived; they nowhere utilize references to the geographic provenance of specimens, or any characters discernible in only one sex, or one stage in life. They attempt to provide, by the standard series of alternative choices, a means of identifying species belonging to extremely close-knit groups. Further, in framing the keys I have attempted as far as possible to steer clear of color characters. *Anolis* colors fade in all preservatives known to date, even if they are not completely annihilated; in some cases I have been forced to resort to them, but they are of a sort that most preserved specimens should still show. Assuredly, the *Anolis* would (and do) identify each other on the basis of color: all of them differ sharply from each other both in hues and patterns. Certainly, the biology of interspecies relationships does not depend on the correct assessment of the posterodorsal terminus of the prenasal with respect to the naris, or the correct counting of the number of midventrals in the standard distance, by living lizards in the field. In addition, such characters as throat fan size (notable in males only) or the manner in which sexual dimorphism is expressed (scales, or size, or color) are of major evolutionary and biological importance, but they are disbarred here on the grounds that the user of the key may not have both sexes in hand. Lastly, even seemingly insignificant damage to specimens, such as nose rubbing so common in captives, or twisting in preservative, may render some of the characters undeterminable.

These keys will not aways work. Fortunately, perhaps, they do seem to work best when separating geographically proximate species. As an example, the shape of the prenasal scale, which neatly separates all races of *A. oculatus* collectively from all races of its closest neighbor, *A. marmoratus*, collectively, can be confusing in geographically distant forms like *A. acutus* and *A. wattsi*, simply because the sutures in the prenasal area may be incomplete; I can only recommend that every lizard has two sides: if the character fits neither description in a couplet on one side of the animal, try the other side before giving up. Some old specimens were twisted so effectively by their original bottlers that the ear opening on one side may be stretched all out of original shape; on the other side it may be nearly squashed shut. I recommend that the height/width ratios of both sides be averaged.

Keys are not provided for subspecies, but the diagnoses written for them are directly comparable within the particular species in question; that is, within a particular, polytypic species I cite, in the diagnosis of each subspecies, the condition of each character that is diagnostic of any subspecies of that species. The subspecies diagnosis, therefore, gives the condition of all identifying features within the species, even if not a unique character of the subspecies in question; this makes identification merely a matter of finding the particular description (= diagnosis) that fits.

SYSTEMATICS

> *Anolis* must be known intimately—anatomically, ecologically, ethologically—in all its relationships within and between species, if the many puzzles the genus poses are to be solved.
>
> —E. E. Williams (1959)

A plethora of *Anolis* forms inhabits the Lesser Antilles; many are very geographically restricted, but all are abundant where found. There are tiny, geckolike rock anoles; medium-sized anoles of generalized habits and ubiquitous habitat; brilliantly colored forms of the dense jungles that rival birds in hues; dull, somber forms ideally camouflaged on a dung hill; and there are grand giants. The standard criterion for what constitutes a "giant" anole has usually been the existence of individuals exceeding 100 mm snout-vent length. This is an arbitrary criterion, but in the Lesser Antilles, it seems to provide a distinction that is almost uncanny. Thus, in the forms named *bimaculatus*, *leachi*, *ferreus*, *griseus*, and *richardi*, the populations seem composed of two size classes: females and juveniles below about 80 mm in average snout-vent length, and old adult males exceeding 100 mm snout-vent length. This existence of a distinctly bimodal distribution of sizes was what led Etheridge (1964) to postulate the existence of three species in the late Pleistocene of Barbuda: the smallest class was apparently *A. wattsi forresti*, the two larger classes represented female and juvenile *leachi* and old adult male *leachi*, separated by an apparent gap. This bimodal size distribution in species where some individuals exceed 100 mm snout-vent is probably explained by a combination of two factors: (1) a strong sexual dimorphism with respect to size, and (2) predators.

The first factor is quite apparent in *bimaculatus* and *leachi*, but less so in the others—i. e., in most of the "giant" forms occasional females get large, thus demonstrating the potentiality for large size in both sexes (females never get quite as large as males, of course).

With respect to the second factor, *Falco sparverius* is the most commonly observed predator on Lesser Antillean anoles. South of St. Lucia the effect of this bird may be somewhat usurped by the common snake, *Mastigodryas boddaerti*: sparrow hawks are not so common in St. Vincent, the Grenadines, or Grenada as elsewhere. In any case, neither the falcon nor the snake is large enough to tackle very large anoles, and thus, once over a certain size, an individual anole may be relatively free from predation. This supposition agrees with the observation that some forms (*A. luciae, A. roquet, A. extremus, A. nubilus, A. oculatus*, and some of the *A. marmoratus* races other than *ferreus*) that exceed 80 mm but not 100 mm snout-vent, fail to show a striking bimodality with respect to size.

It would appear then, that once an anole got beyond the *ca.* 100 mm snout-vent threshold it would be quite likely to survive for a long time; contrarily, individuals approaching the 100 mm mark might be more prone to predation (big enough to be obvious, but still small enough for predators to cope with). Therefore, in species where there exists individual potentiality for size exceeding 100 mm snout-vent, there seem to be many more individuals, at a given time, beyond that mark than there are immediately (80–99 mm) below it.

The 100 mm standard for the class of "giant" anoles may thus have some real biological significance in Lesser Antillean forms, and may be less arbitrary as a measure than has been previously thought.

Underwood (1959) recognized three groups of Lesser Antillean *Anolis:* the *bimaculatus* group, the *roquet* group, and the *wattsi* group. Etheridge (1959) put *wattsi* into his *bimaculatus* series, and put the entire *roquet* group in with their close South American relatives of his *latifrons* series. That arrangement agrees with subsequent work done by Gorman and Atkins (1968a and b, and papers therein cited) on chromosomes, Gorman and Dessauer (1966) on blood proteins, and Gorman (1968) on behavior. The Etheridge arrangement is the one followed here. None of the scale characters cited by Underwood (1959) as separating his groups holds up when large numbers of specimens are considered, and I find no others that will separate the *bimaculatus* and *roquet* groups as entities. This is inconvenient, perhaps, for the museum curator, but not really a serious problem. Members of the *roquet* group of *Anolis* do not look like those of the *bimaculatus* group; as indicated by Duméril and Bibron (1837) with the name "*Anolis alligator*" (a synonym for *A. roquet*), they have a distinctly crocodilian look. Even the short-nosed species, such as *A. richardi* or *A. griseus*, conform, and look like some of the caimans.

Unfortunately, a considerable familiarity with Lesser Antillean anoles is required before one can separate members of the two groups on the basis of general appearance. The next simplest method of separation is geographic: the *bimaculatus* group occupies the islands from St. Croix southward to Dominica; the *roquet* group occupies the islands from Grenada northward to Martinique. The sole case of geographic overlap results from the tiny, and obviously introduced, colony of *Anolis wattsi* (*bimaculatus* group) in Castries, St. Lucia (a *roquet* group island).

For those who lack both familiarity with the lizards and geographic data, distinguishing definitions may be devised. Etheridge (1959) separated all members of the *bimaculatus* series (both Greater and Lesser Antillean) from all members of his *latifrons* series (Lesser Antillean *roquet* group and South American relatives) by the single character of number of parasternal chevrons attached to dorsal ribs. Gorman's (1968) chromosome data provide a method of separating Lesser Antillean *bimaculatus* group members from one of their Greater Antillean relatives, and head proportions will eliminate the remainder.

Similarly, autotomy septa in the caudal vertebrae separate the Lesser Antillean members of the *roquet* group from most other members of the *latifrons* series. Unfortunately, there are extralimital *latifrons* series *Anolis* that are either members of the *roquet* group itself (*bonairensis, blanquillanus*) or are so poorly known osteologically at the present time (*agassizi*) that a geographic clause must remain in my definition of the group. In short, then:

Lesser Antillean *Anolis* of the *bimaculatus* group have: (1) three parasternal chevrons attached to dorsal ribs, (2) an $X_1X_1X_2X_2$ (female) and X_1X_2Y (male) trivalent sex inheritance system, and (3) a moderately long snout: the standard distance is greater than 125 per cent of the distance from the center of the eye to anterior edge of the ear. The *roquet* group (and all *latifrons* series anoles) are eliminated by character (1). *Anolis evermanni,* of Puerto Rico, lacks character (2). All the remaining *bimaculatus* group members (the *stratulus-distichus* complex) are shortheaded and eliminated by character (3).

The Lesser Antillean *Anolis* of the *roquet* group have as follows: (1) four parasternal chevrons attached to dorsal ribs, (2) no karyotypic sexual heteromorphism, (3) functional autotomy septa in the caudal vertebrae, and (4) they occur east of 63° W longitude.

As noted above, three extralimital *Anolis* of the *latifrons* series agree with members of the *roquet* group in having functional caudal autotomy septa: *A. agassizi,* of Malpelo Island, eastern Pacific; *A. bonairensis,* of Bonaire, and *A. blanquillanus* of Blanquilla, both off the coast of Venezuela west of 64° W longitude. I have seen none of these forms in life. Etheridge (personal communication) reports that *agassizi* is osteologically distinct, and under study. Gorman and Dessauer (1966) and Gorman and Atkins (1967) show *bonairensis* to be distinct in karyotype and blood proteins from its close relatives in the Lesser Antilles. *A. blanquillanus* was described by Hummelinck (1940) as a subspecies of *A. bonairensis.* Gorman and Atkins suggest that *blanquillanus* "is the living intermediate between *luciae* and *bonairensis*"; but there is no karyotypic or biochemical evidence on this point. Removal of the geographic clause in the above definition must await the collection of further information.

Underwood (1959) recognized thirteen forms of Lesser Antillean *bimaculatus* group anoles, and divided them among six species (one unnamed). Of these, one (*bimaculatus*) was credited with six subspecies, another (*speciosus*) with two; the remainder were considered monotypic.

Anolis wattsi was placed in a group by itself on the grounds that it possessed a double row of enlarged middorsals, keeled ventrals, and narrow digital dilations. Actually, all Lesser Antillean members of the *bimaculatus* group possess a double row of enlarged middorsals (including *sabanus,* noted by Williams, 1962a, as not having such scales). Underwood did not regard *Anolis acutus* as being Lesser Antillean, but keeled ventrals are widely distributed among such *bimaculatus* group forms as *lividus* (listed as a subspecies of *bimaculatus* by Underwood, 1959), *marmoratus,* and *oculatus. Anolis acutus* and *A. sabanus* bridge the gap in digital dilation width between *A. wattsi* and the other Lesser Antillean members of the group. Gorman and Atkins (1968) have shown that *wattsi* is karyotypically similar to *bimaculatus, gingivinus, sabanus, marmoratus,* and *lividus,* but different from either *acutus* or *oculatus*—which are very different from each other karyotypically; both, though, may show very heavy ventral keeling. A large amount of fresh material, with color notes and field sketches made from life, has been accumulated, principally by me, since Underwood's (1959) paper.

I have restored *A. wattsi* to the *bimaculatus* group. *Anolis oculatus* has been subdivided into four races (Lazell, 1962); *Anolis marmoratus* now includes six forms listed by Underwood as members of different species, and six additional forms as well (Lazell, 1964a). *Anolis nubilus* Garman (1887) was resurrected from provisional synonymy to subspecies status under *bimaculatus* by Williams (1962a), and is here reinstated as a full species. *A. gingivinus* was returned to species status (Lazell, 1964c). *A. sabanus* Garman (1887) is here returned to species level. *A. acutus* of St. Croix is included in this account.

In synthesis, then, the *bimaculatus* group of *Anolis* in the Lesser Antilles consists of a complex of forms distinct from their Greater Antillean relatives. Most of them are dichopatric, and no more than three full species have ever been collected together on the same island; however, twenty-six are arranged below in nine full species. Only *Anolis bimaculatus leachi* has remained unaffected by nomenclatorial changes since the last revision of these forms (Underwood, 1959).

In the Lesser Antillean members of the *bimaculatus* group, the males possess conspicuously enlarged postanal plates; these are absent in females. Remarks made below on sexual dimorphism in squamation do not include this universal feature of the group.

The Lesser Antillean members of the *roquet* group have been reviewed extensively with respect to display behavior (Gorman, 1968), karyotypes (Gorman and Atkins, 1967), and blood proteins (Gorman and Dessauer, 1966). The general aspects of the zoogeography of the best known forms are reviewed by Gorman and Atkins (1968b). None of these works is taxonomic in nature or intent, and none resorts to anatomical features at a level higher than karyotype. The last revision of these forms is that of Underwood (1959). He recognized nine forms in three full species: *roquet* (with three subspecies), *trinitatis* (with four subspecies), and *richardi* (with two subspecies). Gorman and Atkins (1968b, and works cited therein and above) regard Underwood's *roquet* as confounding three distinct forms (*roquet, extremus,* and *aeneus*) and including a fourth (*cinereus*) not separable from *aeneus*. They regard *trinitatis* of Underwood as confounding two very distinct forms (*trinitatis* and *luciae*), each of which they consider monotypic (i. e., *vincenti* equals *trinitatis; procuratoris* equals *luciae*). They regard *richardi* and *griseus* as distinct. My work substantiates the views of Gorman and Atkins as a skeletal arrangement; five new parapatric races of *Anolis roquet* are described, so not even *Anolis roquet roquet* of Underwood remains as in his usage.

All *Anolis* seem to be basically insectivorous; dietary niche segregation between sympatric species must, therefore, depend on the habitat in which prey is hunted, or the size of the prey, or both. Both Gosse and Barbour reported *Anolis garmani* eating vegetable matter, and Grant implied disbelief (all in Lynn and Grant, 1940: 84–85). I have observed that many species of *Anolis* commonly eat vegetable matter, and have watched *A. garmani* (in Jamaica) eating green leaves, *A. bimaculatus* biting pieces out of *Opuntia* fruits, and *A. griseus, A. richardi,* and *A. aeneus* eating berries (the latter two together); details for all but the first mentioned are given in the species accounts.

A KEY TO LESSER ANTILLEAN *ANOLIS* OF THE *BIMACULATUS* GROUP

1\. a. Prenasal subrectangular, not extending to the level of the naris .... *oculatus*
   b. Prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris 2
2\. a. Midventrals smooth or weakly keeled 4
   b. Midventrals strongly keeled 3
3\. a. Interparietal in contact with supraorbital semicircles, or, if separated by one scale, then more than 23 midventrals in standard distance, or, if separated by two scales, then more than 28 midventrals in standard distance .... *acutus*
   b. Not as above .... *wattsi*
4\. a. Width of ear opening contained in height 2.3 or more times 7
   b. Width of ear opening, at middle of ear, contained in height of ear opening 2.2 or less times 5
5\. a. 26 or more subdigital lamellae under the second and third phalanges of the fourth toe 6
   b. 25 or less subdigital lamellae .... *gingivinus*

6\. a. Male with large plain white fan; female with white spots or streak over hind limb .... *nubilus*
   b. Male with small marked or colored fan; female without white spots or streak over hind limb .... *bimaculatus*
7\. a. Males with very large, very dark spots covering dorsal surfaces; females with smaller, more mottled, but very definite dark spots laterally .... *sabanus*
   b. Not spotted as above 8
8\. a. Eyelids yellow to red, but no dark vermiculations or speckles on nape .... *lividus*
   b. Any combination not covered by 7 or 8a (that is, males with dark spots confined to sides or anterior body; or females without large, dark, mottled, lateral spots; or with yellow to red eyelids *and* nape speckling; do not despair, there are only 12 races) .... *marmoratus*

KEY TO THE *ANOLIS* OF THE *ROQUET* GROUP

1\. a. Enlarged sublabials extend posteriorly beyond the posterior level of the orbit .... *luciae*
   b. Enlarged sublabials terminate below eye 2
2\. a. Scales of the supraorbital semicircles arranged so that four or fewer abut, or, if more, then interparietal separated from supraorbital semicircles 3
   b. Not as above 4
3\. a. Middorsals in ten per cent of the snout-vent length 11 or less (8–11) .... *griseus*
   b. Middorsals in ten per cent of the snout-vent length 12 or more (12–15) .... *richardi*
4\. a. Dorsals in standard distance 37 or more .... *trinitatis*
   b. Dorsals in standard distance 35 or less 5
5\. a. Axilla without dark pigment .... *aeneus*
   b. Axilla with dark pigment 6
6\. a. Head relatively broad: width between eyes across supraorbitals at narrowest point contained in standard distance less than four times .... *extremus*
   b. Head relatively narrow: width between eyes contained in standard distance four or more times .... *roquet*

Anolis acutus Hallowell

Anolis acutus Hallowell (1856: 228)
Anolis newtoni Günther (1859: 212)

Type. None designated. Apparently none of Hallowell's original material is still in existence: I personally searched both the collection and the catalogues of the Academy of Natural Sciences of Philadelphia; Edmond Malnate (personal communication) is of the opinion that if no specimen can be found on the shelves, or in the catalogues, none is there. The description given by Hallowell would fit any Lesser Antillean *Anolis* of the *bimaculatus* group with keeled ventrals, and certainly fits *acutus.* Because the name is in standard usage for the St. Croix anole (e. g., Gorman, 1968, and works cited therein; Maldonado and Oritz, 1966), I feel that no neotypic designation is presently required.

Type locality. Unknown (Hallowell gives "Cuba?"). Here restricted to Christiansted, St. Croix, where this species is abundant and easily obtained.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals sharply keeled; interparietal in contact with supraorbital semicircles, or, if separated by one scale, then more than 23 midventrals contained in the standard distance, or, if separated by two scales, then more than 28 midventrals contained in the standard distance. (See relationships, below.)

Squamation. One hundred seventeen specimens (76 males, 37 females, and 4 juveniles) are similar to other Lesser Antillean *bimaculatus* group anoles, except in the following features: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 23–35 (average 30) are contained in the standard distance at midbody. The middorsals are keeled or tectiform and imbricate or subimbricate in males, though sometimes quite inimbricate in females; there are 18–25 (average 21) middorsals in the standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size; there are 38–48 (average 43) dorsals in the standard distance six scale rows lateral to the dorsal midline at midbody. The subdigital pads are of the "raised" type of Boulenger (1885). There are 19–26 (average 23) subdigital lamellae beneath the second and third phalanges of the fourth toe.

Coloration. Males are basically brown, but vary from ash or pale olive-green to chocolate, frequently in the same individual. Color change to darker tends to bring out an irregular pattern of slatey, transverse mottlings; concomittantly, fine ashy-white frosting or speckles usually develop. The orbital skin may be undistinguished, or vary from dull yellowish to faintly reddish. The ventral surfaces, from chin to tail, are pale and variably suffused with yellow; dark mottling usually appears along the lateral belly, at least, though it may be highly inconspicuous in the pale color phase. The throat fan varies from virtually white to dull grey-green, and has a yellow to orange-red blotch near (but not at) the anterodistal edge. The fan scales tend to correspond to the ground color of the fan, and thus contrast to the brighter color in the blotch area.

Females are usually brown with a variably bold ladder or striped middorsal pattern and a variable flank stripe; they can turn virtually patternless green-brown or grey-brown. The ventral yellow tends to be more extensive and brighter in females than in males; this situation also occurs in *Anolis gingivinus* (see below).

There is something of a geographic element in color variation. Some individuals from Green Cay and Buck Island appeared dingier or duller than those from Christiansted; the same was true of some specimens from the interior, e. g., Creque Dam. The reddest fan blotches were noted on Buck Island, the reddest orbital skin on an individual from Creque Dam (JDL 77). Buck Island specimens sometimes have bold, light flank stripes, even apparent in males. Some specimens of both sexes in the northwestern part of St. Croix (e. g., Hams Bluff Coast Guard Station and Creque Dam) show a yellowish dorsal wash. Specimens from xeric, coastal areas (e.g., East Point or Sandy Point, opposite extremes of St. Croix) tend to be paler than those from more mesic areas. A male from East Point (JDL 61) turned "a very pretty ashen-grey with a decidedly pinkish tinge" when handled; it had previously been olive-drab.

Adult *Anolis acutus* are shown on Plate 1.

Size and sexual dimorphism. Males of *Anolis acutus* attain 65 mm snout-vent length (JDL 51; S shore, Buck Island); females attain 48 mm (JDL 49, Green Cay, and JDL 62, East Point). Males as small as 48 mm (JDL 61, East Point) appear to be sexually mature; the presence of eggs in the oviducts demonstrates the maturity of females as small as 38 mm (JDL 74, Hams Bluff Coast Guard Station).

The standard distance is 18–22 (average 19) per cent of the snout-vent length in males, and 18–20 (average 19) per cent of the snout-vent length in females. Although there is not an average difference in significant figures, more accurate measurements (e. g., snout-vent to tenths of a millimeter), or larger samples, might show a faint dimorphism.

Sexual dimorphism is well developed in both coloration and average adult size. It is not, however, nearly so striking in either respect as in some other Lesser Antillean forms. This is in keeping with the postulated position of *Anolis acutus* in *bimaculatus* group phylogeny (see below).

Population structure and ecology. This is a genuinely ubiquitous anole. Most foraging, in both sexes, is done on the ground, and perches are selected from just above ground level to at least ten feet; females and juveniles tend to perch closer to the ground than do adult males.

Retreat behavior may be either up, with the intention of escaping out of reach of the collector, or down into cavities and crevices. In a wooded, fairly rugged area, like that around Creque Dam, *Anolis acutus* can be maddeningly effective at both techniques.

Two eggs (MCZ 46238; no precise locality) measure 10.5 × 7.0 mm and 11.0 × 7.6 mm.

The sex ratio appears to be balanced, although there is a bias for male captures on the part of collectors (including myself). I have observed copulation in June and February, and assume breeding behavior occurs through the year. Judging from the fact that females characteristically contain one large egg in one oviduct and one small one in the other, it is reasonable to assume that eggs are laid singly at intervals of a few weeks. In all of these respects, *Anolis acutus* seems typical of Lesser Antillean *Anolis* as a whole.

Distribution. Anolis acutus is confined to the St. Croix Bank, where it is abundant and infradispersed throughout St. Croix itself and on the coastal cays. MCZ 10339(5), collected by G. K. Noble and labelled "St. Claude, Guadeloupe" are a simple case of label switching: MCZ 10428–37, also collected by Noble, bear the locality datum "St. Croix," but are *Anolis marmoratus* typical of the St. Claude population.

Relationships. Anolis acutus, like all other Lesser Antillean *bimaculatus* group anoles, shows male chromosomal heteromorphism (Gorman, 1965; Gorman and Atkins, 1966, 1967, 1968a and 1968b). Characteristically, in this group, 2n = 29 in males, 2n = 30 in females. *Anolis oculatus* is an exception where 2n = 31 and 32. *Anolis acutus* resembles *oculatus* in having 2n = 31 and 32, for males and females respectively, but the morphology of the karyotype is very different: "There are six large pairs of metacentric macrochromosomes, and then a small seventh pair somewhat intermediate in size between the macro- and microchromosomes." (Gorman and Atkins, 1968b). This contrasts to the situation in *oculatus* and all other Lesser Antillean members of the *bimaculatus* group, which have at least nine pairs of macrochromosomes. It is, however, similar to that of *Anolis stratulus* of the Puerto Rico Bank, and not far different from other Greater Antillean members of the group. The work of Gorman and Atkins thus argues for the phylogenetic intermediacy of *acutus* between the two geographic subgroups: it has the sex chromosome heteromorphism of its Lesser Antillean relatives, but resembles its Greater Antillean relatives in other aspects of karyotype morphology. It is, of course, geographically intermediate as well. Usually, Greater Antillean *bimaculatus* group anoles have a throat fan with a bright, central blotch color contrasted to a border color; Lesser Antillean forms do not. *A. acutus,* with its yellow to orange-red blotch, resembles its western relatives in this respect.

Despite karyotype and color distinctions, *A. acutus* is strikingly similar in morphology to *A. wattsi,* on the one hand, and *A. sabanus* on the other. It differs from the latter principally in having keeled, rather than smooth, ventrals; from *A. wattsi* (as can be seen from comparing species diagnoses) *acutus* is hardly distinguishable on squamation. This is in part due to the squamational diversity of the four races of *wattsi,* but in large measure reflects a real similarity; *A. wattsi* is probably the closest relative of *acutus.* The difficulty in diagnosing these forms also results from the fact that smaller scaled individuals of *acutus* have smaller scales all over; small ventrals are coupled with small head scales. The diagnosis must take this into account.

Anolis acutus is intermediate in size between *A. wattsi,* on the one hand, and the larger forms, like *bimaculatus* itself, on the other. It has not gone in for spectacular sexual dimorphism in scales and color (as has *sabanus*) or spectacular dimorphism in size (as has *bimaculatus*); it shows a balance of the two. Like its geographically distant neighbors, *marmoratus* and *oculatus* (also the sole anoline inhabitants of their ranges), *A. acutus* is ubiquitous and unspecialized in habitat.

All considered, it is tempting to speculate that all Lesser Antillean *bimaculatus* group anoles derived from Greater Antillean stock via an ancestor so close to the present form that, if I had a specimen before me, I would pronounce it *Anolis acutus*. That I have succumbed to this temptation will be evident from the general evolutionary discussion provided for the *bimaculatus* group below.

Anolis wattsi Boulenger

Anolis wattsi Boulenger (1894: 375)

Type. BMNH 1946.8.29.12–13 (*fide* Underwood, 1959: 217).

Type locality. "Antigua"; here restricted to the capital city of St. John's, Antigua, where this species is abundant and displays unequivocally the characteristics of the nominate subspecies.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals sharply keeled; interparietal separated from supraorbital semicircles by three or more scales, or, if by only two, then with less than 28 midventrals in the standard distance, or, if by only one, then with less than 23 midventrals in the standard distance.

Remarks. Anolis wattsi, as here understood, is an amalgamation of four, quite different, dichopatric forms. In two cases there is evidence of apparent character approach between two geographically approaching forms. Because ecological conditions in each case also become increasingly similar in concordance with geography, a case might be made for regarding the similarities of the anoles in the relevant areas as convergence in distinct species. Because several characters are involved in each case, and because some of these characters are not ostensible adaptations to ecological conditions, I regard the apparent character approach as evidence of evolutionary continuity, and therefore, as evidence of conspecificity.

In one case there is apparent divergence in a major diagnostic character concordant with geographical approach. If the two forms involved were absolutely distinct on the basis of any one of the several characters in which they differ, I would regard this character divergence as compelling evidence that full species level has been reached. In this case, however, though the differences separate more than 95 per cent of the specimens, absolute distinction has not been reached. On the basis of present information, therefore, I have little choice but to regard these forms as still conspecific.

There is definite evidence within one form of morphological divergence and distributional change since 1922. Clearly, the arrangement offered here of four subspecies is only temporary; speciation is here in a vividly dynamic state.

The deployment and major features of the four races are indicated in Figure 3. Details are presented under the relevant forms below; a discussion including the possible evolutionary history of the complex follows the subspecies accounts.

Anolis wattsi wattsi Boulenger

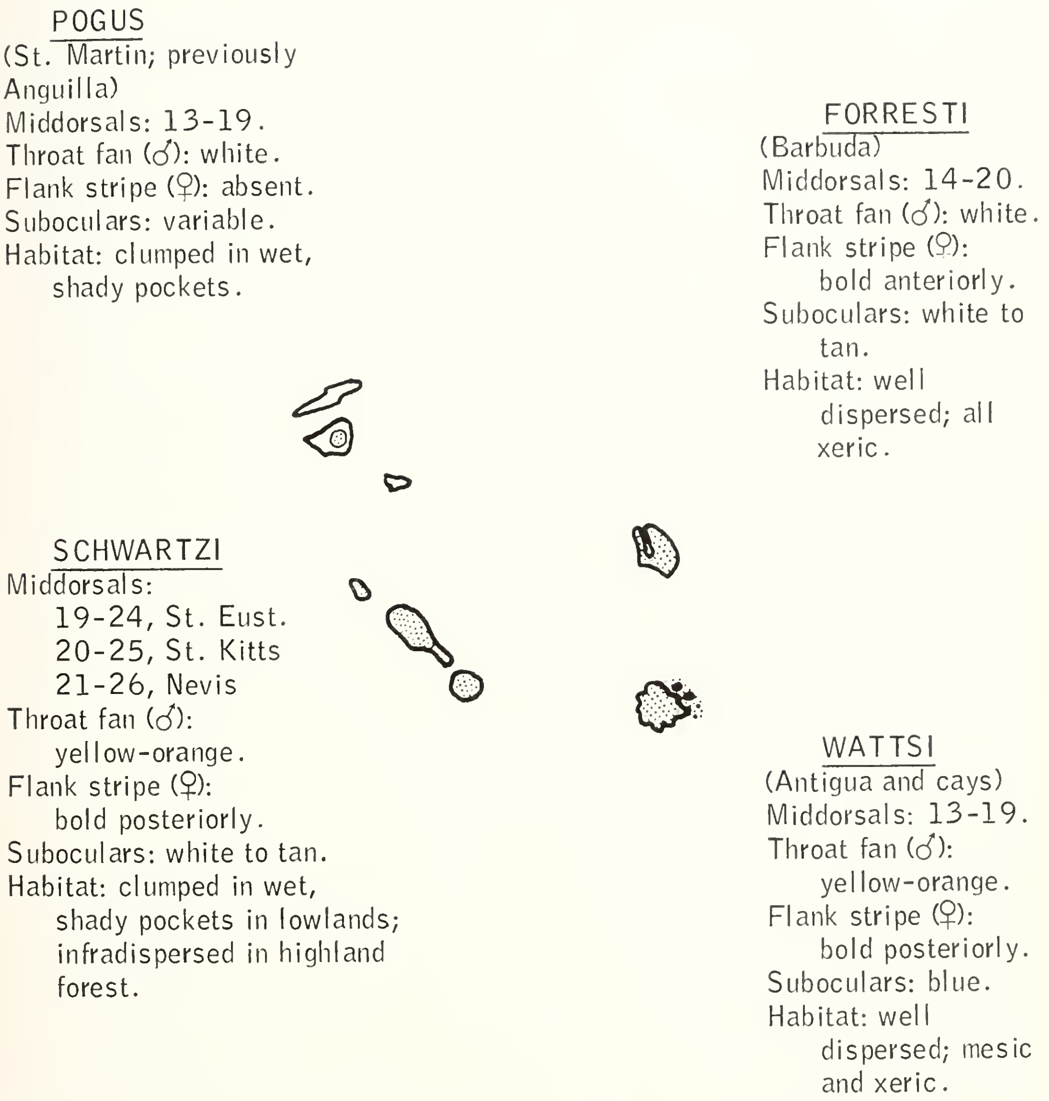
Anolis wattsi Boulenger (1894: 375)

Type. BMNH 1946.8.29.12–13 (*fide* Underwood, 1959: 217).

Type locality. St. John's, Antigua, by present restriction (see above).

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance at midbody 13–19; male with orange-yellow throat fan; female with variable flank stripe always boldest posteriorly; suboculars usually blue.

Squamation. One hundred seventy-four specimens (98 males, 71 females, and 5 juveniles) are similar in squamation to other Lesser Antillean *bimaculatus* group



POGUS
(St. Martin; previously Anguilla)
Middorsals: 13-19.
Throat fan (♂): white.
Flank stripe (♀): absent.
Suboculars: variable.
Habitat: clumped in wet, shady pockets.

FORRESTI
(Barbuda)
Middorsals: 14-20.
Throat fan (♂): white.
Flank stripe (♀): bold anteriorly.
Suboculars: white to tan.
Habitat: well dispersed; all xeric.

SCHWARTZI
Middorsals:
19-24, St. Eust.
20-25, St. Kitts
21-26, Nevis
Throat fan (♂): yellow-orange.
Flank stripe (♀): bold posteriorly.
Suboculars: white to tan.
Habitat: clumped in wet, shady pockets in lowlands; infradispersed in highland forest.

WATTSI
(Antigua and cays)
Middorsals: 13-19.
Throat fan (♂): yellow-orange.
Flank stripe (♀): bold posteriorly.
Suboculars: blue.
Habitat: well dispersed; mesic and xeric.

Figure 3. The deployment and major features of the four subspecies of *Anolis wattsi*. See text.

anoles, except in the following features: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 16–26 (average 20) midventrals are contained in the standard distance at midbody. The middorsals are keeled or tectiform, and imbricate or subimbricate in males. From 13–19 (average 16) middorsals are contained in standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size. There are 35–49 (average 42) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow in most specimens, and are sometimes not clearly of the raised type of Boulenger (1885) and Williams (1963). There are 17–22 (average 20) lamellae under the second and third phalanges of the fourth toe.

Coloration. In life, this is typically a bright and very pretty anole. Males have a basically brown dorsum, usually with a posterolateral green wash, and show faint, darker, transverse bands at least in their darker color phase; darkening seems to be associated with disturbance or capture throughout the range. The chin and snout are suffused with orange, as is the underside of the tail. Sometimes an orange suffusion extends over the posterior dorsum, tail, and hind limbs. The venter is pale to bright yellow, frequently with a green abdominal wash. The throat fan is rich orange-yellow with pale blue, blue-grey, or white scales; the fan scales turn grey in the disturbed phase. The subocular scales are typically bright sky blue; this blue usually extends brightly to the eyelids, and fades into the temporal area. A copper-tarnish green is frequently noticeable on the supraocular disk and sometimes includes the orbit generally.

Females are rich brown to dull grey-brown. There is a pale tan middorsal stripe bordered, and usually interrupted by, dark grey-brown, constituting a striped or ladder middorsal pattern. A pale flank stripe may be present from axilla to groin, but is boldest in the groin region, and usually set off from the ground color by dark grey-brown speckles that frequently coalesce into continuous streaks near the hind limb insertion. The venter varies from cream to yellow; the underside of the tail is yellow to orange. There is no green wash on the trunk. The orange of the chin and snout, and the copper-tarnish green of the orbit, may be reduced from the usual male condition to absence. The suboculars are normally blue, but this color is duller and less extensive than in males.

Although the degree and arrangement of chin spotting with black dots is variable in nominate *wattsi*, and not of diagnostic value, variation in this character is interesting. The mentals, anterior sublabials, and anterior gular scales are nearly white in ground color in preserved specimens (the yellow and oranges fade rapidly). Most Antiguan *wattsi* have small, subcircular, black dots fairly uniformly scattered over these scales. *Anolis wattsi* from the St. Kitts Bank is dingier and darker than the Antiguan form, and its chin spots reflect this difference: large and heavy. *Anolis wattsi forresti* from Barbuda is paler than any other subspecies; chin spots in this form are rather small and centrally located on the scales. Four females of nominate *wattsi* from interior SW Antigua (Body Ponds, MCZ 75697–700) have the large, heavy chin spotting typical of St. Kitts Bank individuals. One male from this same region (Boggy Peak, MCZ 55465) resembles *forresti* of Barbuda in having the spotting centrally located on the scales, and the scale margins relatively free of spots. In this specimen, however, the spots are very large and heavy—not like the fine speckles of *forresti*. The St. Kitts Bank and Barbuda extremes of chin spotting are shown in Figure 4.

Patterns of adult *Anolis wattsi wattsi* are shown on Plate 1.

Size and sexual dimorphism. Males of *A. w. wattsi* reach 58 mm snout-vent length (MCZ 75635, St. John's); females attain 46 mm snout-vent length (MCZ 64336, St. John's). Males as small as 39 mm (MCZ 75705, Johnson's Point) appear sexually mature; the presence of eggs in the oviducts demonstrates the sexual maturity of females as small as 36 mm (MCZ 68914, Gaylor's Estate).

Aside from the striking differences in coloration and pattern (see above), there is only average sexual dimorphism in size in *A. w. wattsi;* at maturity the sizes of the sexes overlap broadly. There is no significant dimorphism in head size. The standard distance is from 16–19 (average 18) per cent of the snout-vent length in both males and females. Williams (1962a) suggested that males have larger scales than females. Subjectively judged, this certainly seems to be true; I did not have enough equal-sized males and females to make a statistically significant objective assessment of this possibility. Since there is no average difference between the sexes in number of middorsal scales counted in the standard distance, I can only surmise that whatever actual differences in scale size exist are fully compensated for by the "crowding" (mentioned by Williams, 1962a), and consequent imbrication, of the middorsals in males.

Population structure and ecology. Barbour (1930b) regarded this form as rupicolous; this is an oversimplification. Although basically rupicolous, *A. w. wattsi* occurs on trees, bushes, and fence posts up to three feet above the ground. It shows a preference for shady stations, but occurs abundantly in very xerophytic regions, occasionally perching at open, sunny stations. Females and juveniles are more terrestrial and, therefore, more rupicolous than adult males; the latter characteristically perch twelve to twenty-four inches above ground level, but forage on the ground.

A. w. wattsi is less than infradispersed, but certainly not clumped; this corresponds to ecological conditions. In shady areas the species abounds; in xeric regions individuals usually are more scattered but find suitable stations wherever rocks or bushes provide even the slightest cover. Sugar cane fields, roads, and pastures provide at least some (though slight) barrier to complete infradispersion.

Retreat behavior in this form consists of ducking into holes and crevices in rocks or tree trunks, or frequently, running under detritus on the ground.

Distribution. *Anolis wattsi wattsi* is abundant all over Antigua in suitable habitats and occurs on every coastal cay that supports more than herb stage vegetation. This form also occurs in Castries, St. Lucia, where it apparently was recently introduced. MCZ 57221–2 and MCZ 58750 plus one untagged, collected by Proctor, bear only the datum "Castries." I, however, found this form only in the Botanical Garden (MCZ 71818–21), and never encountered it elsewhere. It may spread in St. Lucia, as neither of the other anoles occurring there seriously impinges on its basically rupicolous niche.

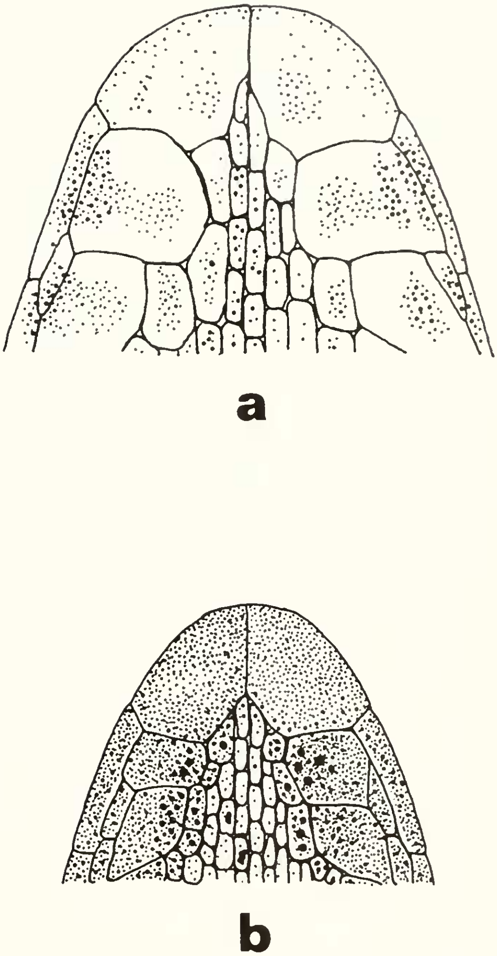


Figure 4. Extremes of pallor and dinginess in *Anolis wattsi* indicated by dark speckling on the mentals, anterior sublabials, and anterior gulars. (A) *A. w. forresti*, MCZ 75724. (B) *A. w. schwartzi*, JDL 209 (Type).

Relationships. Extreme northern Antigua (vicinity of Hodge's Bay), Long, Great

Bird, and Guana Islands (all off the northeast coast) are geographically, and ecologically, closer to the range of the Barbuda form, *A. w. forresti*, than any other parts of Antigua. Individual *wattsi* are sometimes paler in this area than elsewhere in their range. They lack the dinginess of the St. Kitts Bank *wattsi* representative, but, like that form and *forresti* from Barbuda, they may lack bright subocular blue. MCZ 75657, from Parham, and MCZ 75668 from Guana Island (both males from series of ten specimens), are examples. MCZ 75645–51, from Hodge's Bay, vary from the normal, bright condition of *A. w. wattsi* to notably paler, but all fit the diagnostic color characters of the subspecies. MCZ 75719, a male from Long Island (one of series of ten), has a throat fan of light, bright yellow. MCZ 75722, a female from the same Long Island series, has a flank stripe that is boldly accentuated throughout its length; MCZ 84987 and JDL 243, females from Great Bird Island, are similar. I regard these specimens, intermediate between nominate *wattsi* and *forresti* of Barbuda, as demonstrating the conspecificity of the two forms (see *Coloration*, under *A. w. forresti*).

Specimens of nominate *wattsi* from the mesic SW interior of Antigua may be very dark and dingy—thus resembling the *wattsi* representative of the St. Kitts Bank. MCZ 55465, from Boggy Peak, though lacking color notes from life, is clearly an example of this. MCZ 75691–700, from Body Ponds, were collected by me, and are all noted as being dingy in life. Of these, two females, MCZ 75698 and 75700, lack subocular blue, and could not be distinguished from St. Kitts Bank material on the basis of color. MCZ 75646, a male from Hodge's Bay, is an example with rather small scales; there are 19 middorsals contained in the standard distance at midbody. Five other specimens from scattered localities also are included in the range of scale size variation of specimens from St. Eustatius, the northernmost island of the St. Kitts Bank. Because overlap with St. Kitts Bank *wattsi* representatives occur in both coloration and squamation, albeit in a tiny number of specimens, I regard these forms as conspecific.

A. w. wattsi overlaps the scale size of the St. Martin (Anguilla Bank) representative of the species, but scarcely resembles it in other respects.

The only other previously named *wattsi* representative has been named twice and synonymized between the namings. It should be known as:

Anolis wattsi forresti Barbour

Anolis forresti Barbour (1923: 4)
Anolis wattsi, Underwood (1959: 217)
Anolis alter Williams (1962a: 463)

Type. MCZ 16170, W. R. Forrest coll., no date.

Type locality. "Barbuda"; here restricted to the major town, Codrington, Barbuda, where this form abounds, and displays unequivocally the characteristics of the taxon.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance 14–20; male with virtually white throat fan, and no dark, mossy, lateral body bars; females with variable flank stripe always boldest anteriorly; suboculars bluish white to pale tan.

Squamation. Eighty-two specimens (49 males, 31 females, and 2 juveniles) are similar in squamation to other Lesser Antillean *bimaculatus* group anoles, except in the following features: the prenasal is posterodorsally elongate: it always extends to the anterior level of the naris and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 17–23 (average 20) midventrals are contained in the standard distance at midbody. The middorsals are keeled or tectiform, and imbricate or subimbricate in males. From 14–20 (average 17) middorsals are contained in the standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size. There are from 35–45 (average 39) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow in most specimens, and are sometimes not clearly of the raised type. There are 17–22 (average 20) lamellae under the second and third phalanges of the fourth toe. In squamation this form is essentially similar to the nominate race.

Coloration. In life, this is a rather colorless, drab, normally pale, grey-brown anole. There may be a faint posterior wash of green, giving some specimens an olive drab color. Males normally show little if any marking, except faint darker grey-brown transverse bands when disturbed; just the opposite occurs: specimens may be normally faintly banded, and become uniform and pale when disturbed. Some males have a general yellowish cast. The snouts of males are usually red-brown or copper tinted; the chin is cream to yellow. The bellies of males are dirty white to light, bright yellow. Usually the belly is brighter posteriorly: those with dirty white anterior venters normally have cream posterior venters; those with cream anteriorly may become light, bright yellow posteriorly. The underside of the tail is similarly cream to yellow. The throat fan is virtually white; there may be an all-over lemon yellow cast, or a faint posterior suffusion of the palest lime green. The scales of the throat fan are not colored differently from the adjacent skin. Color change is so slight that it does not affect the fan or fan scale color. The subocular scales are normally white; pale blue does occur rarely (e. g., MCZ 75743, Castle Rock) and in females and young males the suboculars are often very light tan. A tarnished copper green is frequently noticeable on the supraocular disk, and sometimes includes the orbit generally.

Females are light grey-brown. There is less ventral yellow, as a rule, than in males. The tarnished copper green of the orbital area may be quite absent. A pale tan to ash-grey middorsal stripe is bordered, but usually not interrupted, by darker brown or grey-brown. The flank stripe is well developed and frosty white on the shoulder; it fades out posteriorly, and is never set off by darker bordering pigmentation in the groin.

The pallor of *A. w. forresti* is indicated well by the chin spotting (see Fig. 4). The spots usually are small but, when large, are rather light and greyish. Spots invade the central portions of the mental halves and anterior sublabials from the sides of the head, but do not normally extend onto the anterior, posterior, or median margins of these scales, or onto the gular scales.

The patterns of adult *Anolis wattsi forresti* are shown on Plate 1.

Size and sexual dimorphism. Males of *A. w. forresti* reach 52 mm snout-vent length (MCZ 75726, Codrington); females attain 45 mm (MCZ 75730, Codrington). The smallest male that appears sexually mature is 38 mm (MCZ 75734, Codrington); the presence of eggs in the oviducts demonstrates the maturity of females as small as 38 mm (MCZ 68565, Derby Cave).

Aside from marked differences in pattern (see above) there is only average dimorphism in *A. w. forresti:* at maturity the sizes of the sexes overlap broadly. There is no significant difference in head size: the standard distance is from 17–19 (average 18) per cent of the snout-vent length in both males and females. As in *A. w. wattsi* (see above) whatever difference in scale size exists between males and females must be compensated for by scale crowding in males; the average number of middorsals counted in the standard distance is seventeen in both sexes.

Population structure and ecology. Like *A. w. wattsi*, the subspecies *forresti* is well dispersed throughout its range, though its preference for shade concentrates individuals somewhat. Shade, however, is available wherever there are bushes or rocks, so no real clumping into demes is discernible. Barbuda is, however, far more xeric than most of Antigua; the "wet pockets" that Williams (1962a, b) believed to exist in the sinkholes (called "caves" on Barbuda) are absent (see *Discussion*, below). Like *A. w. wattsi*, males of *A. w. forresti* usually perch no higher than about twenty-four inches and forage on the ground. Females and young are even more terrestrial and rupicolous. Stone walls are a highly favored habitat.

Retreat behavior is similar to that described for *A. w. wattsi*, above.

Distribution. This anole is found throughout Barbuda whenever suitable habitat occurs; it does not penetrate mangrove swamp (extensive in the north) more than a few yards beyond the point where the mangroves actually grow in water, but it does occur along the edges of the swamps.

Relationships. The presence of intermediates in color between nominate *wattsi* and *forresti* in extreme northern Antigua and on the islands off the northeast Antiguan coast is regarded as evidence of the conspecificity of the two forms. *A. w. forresti* resembles the *A. w. wattsi* representative on St. Martin in squamation and male throat fan color, but strong distinction in pattern characters argues against a common derivation of these forms (see *Discussion* following the subspecies accounts, below).

Though nominate *wattsi* and Barbudan *forresti* may be each other's closest relatives, the *wattsi* representative of the St. Kitts Bank is so similar to the nominate form that I did not distinguish them in the field. Dr. Albert Schwartz did, and repeatedly mentioned to me that he felt the St. Kitts Bank populations constituted a valid, different form. It was not until I examined squamation that I realized Schwartz was correct. This new form is therefore named:

Anolis wattsi schwartzi subsp. nov.

Type. MCZ 127088, J. D. Lazell, coll., 15 February 1966.

Type locality. Nevis Peak: South slope above Rawlings, 2500 ft., Nevis.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in standard distance at midbody 19–26; male with orange-yellow throat fan; female with variable flank stripe always boldest posteriorly; suboculars usually white to tan.

Squamation. The following description is of the type (variation in 123 paratypes—77 males, 42 females, and 4 juveniles—is given in parentheses). The type is similar in squamation to other Lesser Antillean members of the *bimaculatus* group (as are the paratypes), except in the following features: prenasal posterodorsally elongate, forming the entire dorsal border of the naris (always extending at least to the anterior level of the naris; sometimes bordering dorsally on a nasal scale that includes the naris). The midventrals are sharply keeled and imbricate. There are 25 (19–28, average 23) midventrals in the standard distance at midbody. The middorsals are keeled (sometimes tectiform) and not imbricate (sometimes subimbricate). There are 22 (19–26, average 22) middorsals contained in the standard distance at midbody. The scales lateral to the middorsals show an abrupt decrease in size. There are 51 (44–60, average 52) dorsals contained in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow (may be as dilated as in some other species, like *A. acutus* or *A. sabanus*), and are of the raised type (may not be clearly so). There are 22 (17–23, average 20) subdigital lamellae under the second and third phalanges of the fourth toe.

There is some geographic variation, indicating a north-south cline, in scale size best shown by the middorsals. Thirty-three specimens (13 males, 18 females, and 2 juveniles) from Nevis have 21–26 (average 24) middorsals in the standard distance at midbody, whereas 18 from St. Kitts (12 males, 5 females, and 1 juvenile) have

20–25 (average 23), and 63 from St. Eustatius (43 males, 19 females, and 1 juvenile) have 19–24 (average 22). The apparent collectors' bias for St. Eustatius (possibly because it is thought of as the "least known" of the three islands?) artificially compromises the difference between *schwartzi* and nominate *wattsi*; it is only in St. Eustatius individuals that overlapping middorsal counts have been found (see *Relationships*, below).

Coloration. In life, the type (an adult male) was dark, dingy grey-brown dorsally and could develop a faint olive tinge with vague transverse markings. The belly was dull, rather metallic looking, yellowish brown. There were orange suffusions on the snout, chin, and underside of the tail. The throat fan was deep orange with dull whitish scales that turned dark grey when the animal was handled. There was a hint of copper-tarnish green in the supraocular disk area, and the suboculars were off-white. The dark, heavy chin spotting is shown in Figure 4.

Preserved, the male paratypes are all very similar to the type. Color notes from life for those specimens collected by me indicate little more variation. All are dull and dingy, and most differ from nominate *wattsi* additionally in lacking subocular blue. Some blue was present in MCZ 75507 and 75509, males from a series of ten from Basseterre, St. Kitts, collected by me.

There is some variation in transverse banding. In about 20 per cent of males from St. Eustatius the anteriormost band, across the neck, is bolder than those on the back. This is also true of JDL 168, a male from Godwin's Gut, 2.5 miles northeast of Lambert's Estate Yard, 1000 feet, in northern St. Kitts. In most other specimens the nape band is no more (usually less) prominent than the back bands, and in some specimens no banding may appear at all. (See *Relationships*, below).

Females of *A. w. schwartzi* are very similar to females of nominate *wattsi*. They are duller and dingier than most Antiguan specimens, frequently lack orange tones, and have pale tan suboculars; but they have flank stripes best indicated in the groin region. They are dull grey-brown dorsally, and from dirty whitish to dingy golden ventrally. The pale tan or grey middorsal stripe is bordered, and frequently interrupted, by dark, slatey grey-brown. The patterns of the type and an adult female paratype are shown on Plate 1.

Size and sexual dimorphism. The type measures 43 mm, snout to vent, and is an adult male. The largest male (MCZ 75497, The Crater of The Quill, St. Eustatius) is 49 mm. The smallest male that appears sexually mature is 34 mm (JDL 212, from the type locality). The largest female examined is 43 mm (MCZ 75500, the Crater of the Quill); the smallest female with eggs in the oviducts is 37 mm (MCZ 75365, also from The Crater of the Quill). Although collectors' bias for St. Eustatius (especially the Crater of the Quill) probably artificially distorts appreciation of the real size range at maturity, it is clear that little sexual dimorphism in adult size is present in this form.

Sexual dimorphism in coloration and pattern in *A. w. schwartzi* is striking, and though the form is duller and dingier, it is basically similar to that in nominate *wattsi*.

In head size, material from Nevis and St. Kitts shows no significant dimorphism. In 13 males and 18 females from Nevis the standard distance is 16–20 (average 18) per cent of the snout-vent length. Variation is less (17–19 per cent) but the average for 12 males and 5 females from St. Kitts is exactly the same. On St. Eustatius, however, significant dimorphism is detectable. In 43 males the standard distance is 18–20 (average 19) per cent of the snout-vent length; in 19 females it is 17–18 (average 18) per cent. The significance of this geographic variation is discussed under *Relationships*, below.

There is not a significant average difference between the sexes in the number of middorsals, even in St. Eustatius specimens. I suppose that head size and scale size are correlated in such a way that larger headed individuals (males) also have larger scales, and that the difference is closely proportional.

Population structure and ecology. All three islands of the St. Kitts Bank have at least remnant rain forest at high elevations; on St. Kitts rain forest is extensive, while St. Eustatius is predominantly xeric. *A. w. schwartzi* occupies rain forest to the seemingly complete exclusion of the otherwise sympatric *Anolis bimaculatus bimaculatus*, and is infradispersed there. In the lowlands, *A. w. schwartzi* is definitely clumped in wet, shady pockets. Clearing for agriculture may have severely restricted suitable habitats, and better dispersion was probably the original condition. Human dwellings and buildings, however, do sometimes provide suitable habitat in the lowlands of the St. Kitts Bank islands, and *schwartzi* frequently is locally abundant around these, as well as in ravines and other naturally wet, shady areas. I was unable to locate any specimens of this form on the very arid, xeric Salt Pond Peninsula of St. Kitts, where no suitable habitat—either natural or artificial—seems to occur.

The rather different ecological relationships and manner of niche segregation observed between *Anolis bimaculatus* and *Anolis wattsi* on the St. Kitts and Antigua Banks, respectively, is discussed under *A. bimaculatus.* The altitudinal differences in population structure in *A. w. schwartzi* reflect the present geographic nature of niche segregation between this form and the largely sympatric *A. b. bimaculatus.* Ridiculous as it may seem, given the spectacular distinctions between these two species, I observed males actually contesting territories in the lowlands, and *A. w. schwartzi* is not always the loser.

Like *A. w. wattsi*, the present race is basically rupicolous, though it frequently perches on trees and shrubs up to three feet above the ground. Male perches are usually 18–24 inches above the ground, and foraging is done on the ground. Females and juveniles are more terrestrial than males. Retreat behavior is the same "into-or-under" type described for the nominate race.

An egg, presumably of this form (no other plausible reptile apparent), measures 10 by 5.7 mm, and was taken with JDL 184–6, south slope of South East Peak at head of West Farm Gut, 2000 feet, St. Kitts, on 12 February 1966.

Distribution. Throughout most of St. Kitts Bank, wherever suitable habitat occurs, up to about 3000-feet elevation; apparently absent from the entire Salt Pond Peninsula of St. Kitts.

Relationships. Anolis wattsi schwartzi is regarded as a subspecies because 10 per cent of the specimens from St. Eustatius agree with 3 per cent of those from Antigua in possessing 19 middorsals in the standard distance. Considering *schwartzi* as a whole, only 5 per cent agree with the 3 per cent of Antiguan specimens that have middorsal counts of 19; this is because specimens of *schwartzi* with such low counts (large scales) have not been found on St. Kitts or Nevis. I examined 124 specimens of *schwartzi* and 174 specimens of nominate *wattsi;* of these 298 specimens 12 had middorsal counts of 19, making a total overlap of 4 per cent. The other characters, like dinginess (as indicated by chin spotting) and subocular blue, in which these two forms differ markedly are not so readily quantified, but seem to show similar, very small percentages of overlap.

Antigua is not much further away from Nevis than is St. Eustatius (see Fig. 6), and Nevis *schwartzi* are more different from Antigua *wattsi* than are St. Eustatius *schwartzi.* Rather than interpreting this fact as character divergence between nominate *wattsi* and *schwartzi*, I suggest that it may indicate evolutionary continuity between *schwartzi* and the *wattsi* representative north of the St. Kitts Bank on St. Martin. This form's range is about as far away from St. Eustatius, geographically, as Nevis is, and as one proceeds towards it from Nevis to St. Eustatius, *A. w. schwartzi* approaches the new St. Martin form's characters not only in scale size, but in two other respects as well: (1) an increased tendency for the neck band to be well developed, and (2) the appearance of sexual dimorphism in head size. Character approach in these three respects, concordant to geographic approach, leads me to regard the St. Martin *wattsi*-like anole as a subspecies.

I collected fresh specimens—the first, apparently for four decades—in St. Martin in 1964. Noting their distinctive characters, I christened them with a brief, comparatively euphonious name that, according to the finest classical lexicons available to me, means nothing at all. Since that time, several other herpetologists have come to refer to this form by my "manuscript" name, and no reason exists to alter it. There follows an account of this, the last and northernmost, member of the *wattsi* complex.

Anolis wattsi pogus subsp. nov.

Type. MCZ 127052, J. D. Lazell, coll. 7 February 1966.

Type locality. Columbier Valley, French St. Martin.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance 13–19; male with virtually white throat fan and dark, mossy, vertical lateral bands; female with no flank stripe; suboculars sky blue, rust red, or virtually white.

Squamation. The following description is of the type (variation in 70 paratypes—42 males, 25 females, and 3 juveniles—is given in parentheses). The type is similar in squamation to other Lesser Antillean members of the *bimaculatus* group (as are the paratypes), except in the following features: prenasal posterodorsally elongate, extending beyond the anterior level of the naris, and forming the anterodorsal border of the naris (sometimes forming the entire dorsal border of the naris). The midventrals are sharply keeled and imbricate; there are 19 (14–20, average 18) midventrals contained in the standard distance at midbody. The middorsals are keeled (sometimes tectiform) and subimbricate (sometimes not imbricate). There are 15 (13–19, average 15) middorsals contained in the standard distance at midbody. The scales lateral to the middorsals show an abrupt (sometimes more gradual) decrease in size. There are 38 (35–45, average 38) dorsals contained in the standard distance at midbody six scale rows lateral to the dorsal midline. The subdigital dilations are fairly narrow (sometimes very narrow) and of the raised type (sometimes not clearly so). There are 20 (17–21, average 19) subdigital lamellae under the second and third phalanges of the fourth toe.

I have examined 68 specimens (40 males, 25 females, and 3 juveniles), all from St. Martin, collected by me in 1964 and 1966. In these the scales are larger than in three older specimens (all males) from the Anguilla Bank. In the fresh material there are 13–17 (average 15) middorsals in the standard distance at midbody; in the three older specimens (all males) there are 18, 18, and 19 middorsals in this distance. This difference is significant (p less than 0.05); its biological significance requires careful consideration.

The possibility that this difference results from preservational, or other, distortions in head-body proportions is strongly contradicted: in all three of these specimens the standard distance is 18 per cent of the snout-vent length, slightly less than the overall male average of 19 (see below).

One of the older specimens, MCZ 20986 (with a count of 18 middorsals), bears the data "St. Martin, Dutch West Indies. G. J. H. Molengraaff coll. 1883." The other two, MCZ 16597–7 (with middorsal counts of 19 and 18, respectively), bear the data "Anguilla Id., British West Indies, J. L. Peters coll. 1922." If one accepts these data as true, then Anguilla Bank *wattsi* seem clearly to have changed morphologically since 1922.

Coloration. Color change is far more pronounced and complex in this form than in other subspecies of *wattsi.* The type, an adult male, was grey-brown when first encountered, with clearly visible slatey transverse bands; the bands were narrow where they crossed the middorsum and widened and faded on the flanks; they were faintly bordered by coloration paler than that of the dorsal ground color. On the neck the anteriormost band was very bold, dark grey; it was well set-off by an ash-grey posterior border, and produced a distinctly collared appearance. The head was largely suffused with rust red. The belly appeared dirty white. The throat fan was virtually white, with the vaguest indication of a grey-green wash posteriorly.

When captured, the dorsal ground color paled to warm tan and a definite mustard yellow suffusion spread over the sides. The dark "collar" faded away almost entirely to grey smudges on the side of the neck. The remaining dorsal bands faded out almost to invisibility at the middorsum and along their more lateral, anterior edges; the remaining, posterior edges of each dorsal band darkened to a mossy, slatey greenish —giving the appearance of a pale animal with very dark lateral (not dorsal) bars. The dorsal surfaces of the head became spectacularly suffused with blue; this was a bright, sky blue over the entire orbital and subocular area, and faded anteriorly and posteriorly. The throat fan was wholly unaffected. The chin spots are fairly uniform, but rather light.

The colors of the 39 male paratypes that I collected were very variable. In some, dull greys and browns were the entire dorsal repertoire, and mustard yellow or greenish tints did not appear. In others, blue was well suffused on the head in what appeared to be otherwise the undisturbed color phase; in still others, various combinations of blue or blue-grey on the orbital region and rust or warm brown on the snout were encountered. Many were indistinguishable from the type in head coloration; others reversed the head color change correspondence to the dorsal pattern, but were equally bright in hues. The basic pattern and manner of pattern change, however, was similar in all specimens. The fan and fan scales are not differently colored, and not affected by color change. A tinge of tarnished copper green is usually visible on the supraocular disk.

Females are duller—usually altogether greys and browns dorsally. They pale, and a few show some mustard yellow lateral suffusion, when disturbed; most have either bluish or reddish suffusions on the head, or both. The suboculars are sometimes virtually white. There is no flank stripe at all. Females show a tiny, "pin stripe" middorsal line of dull tan or slightly metallic light brown. Female pattern is more somber, but similar to that of the male.

Ventral color, in both sexes, varies from dirty white or grey to a rather metallic light brown. Especially in females, there may be slatey speckles, smudges, or blotches on the venter. Chin spotting is extremely variable in both sexes, and not diagnostic.

The most boldly marked individuals collected were JDL 142, 146, and 150 (two males and a female from a series of ten), taken in the Grand Fond, Quartier d'Orlean, French St. Martin. Otherwise, there was no hint of divergence indicated in the four (three French and one Dutch) populations sampled.

The pattern, in both phases, of the type is shown on Plate 1, as is the pattern of an adult female paratype in the disturbed phase.

Size and sexual dimorphism. The type, an adult male, measures 44 mm, snout to vent. The largest male examined is 50 mm, (MCZ 20986, the previously noted Molengraaff specimen); the smallest male that appears mature is 39 mm (MCZ 75812, Colombier Valley). The largest female examined is 42 mm (MCZ 75818, Colombier Valley); the smallest female with eggs in the oviducts is 36 mm (MCZ 75825, Colombier Valley). The bias for collecting at Colombier Valley (36 of the 71 specimens) is my own, but it probably does not give a distorted view of size at maturity in this geographically very restricted form. As in other races of *Anolis wattsi*, sexual dimorphism in adult size is here rather weak.

Because females of *pogus* have such tiny middorsal stripes and wholly lack flank stripes, sexual dimorphism in coloration and pattern is here far less than in the other *wattsi* races.

In head size, however, sexual dimorphism is significant. In 43 males the standard distance is 17–20 (average 19) per cent of the snout-vent length; in 25 females it is 16–19 (average 18) per cent. Perhaps remarkably, the number of middorsals counted in the standard distance averages 15 in both sexes. (The three older specimens do not significantly alter this average, even though they have smaller scales.) This must mean either that larger headed males have less crowded scales, or that their scales are longer in close proportion to head size. Comparison of MCZ 75811, a 40-mm male with a middorsal count of 16 and a standard distance 19 per cent of its snout-vent length, and MCZ 75817, a female of the same size, with the same middorsal count, and a standard distance 17 per cent of the snout-vent length, indicates (albeit not wholly objectively) that the latter alternative is true: the male's middorsals are clearly larger, not at all less crowded. Perhaps the simplest (though certainly not the only) explanation of this fact is to postulate that head size and scale size are pleiotropic effects of the same genetic unit. Simple linkage of two different genetic units might produce more varied results than those observed, but is also possible.

Population structure and ecology. Diagnostic of Williams' (1962a) "*Anolis alter*" was occurrence in pocket populations in wet forest remnants. Ironically untrue of *A. w. forresti* (= *alter*), this is precisely the case in *A. w. pogus.* Locality designations like "Colombier Valley" and "Grand Fond" give an impression of large areas; actually, these places are small ravines: pockets of wet vegetation and shady stones quite comparable in total area to a football field. It is in these wet forest remnants that *A. w. pogus* abounds. These pockets, and *pogus*, occur today only on one Anguilla Bank island: St. Martin. No doubt, this form, or its immediately ancestral stock, occurred on Anguilla. There are specimens (MCZ 16596–7) to prove it, and such localities as Katouche Bay and Mango Garden were certainly once wet vegetation pockets. Charcoal burning or agriculture has totally devastated these areas, leaving eroded gullies and scraggly thornbush. I hoped that a few *pogus* might survive in cave entrances at Katouche Bay, or elsewhere along the northern coast of Anguilla, but despite an exhaustive search in February, 1966, I could find none. If *A. w. pogus* ever occurred on St. Barts, its demise there has been effectively the same, for no habitat comparable with that on St. Martin is present there today.

I sampled four pocket populations of this form in ravines selected for their comparatively large size and geographic coverage of the interior of St. Martin. There are perhaps a dozen other habitable pockets in the total subspecies range, which I estimate at a maximum of 22 square kilometers. On the ridges separating the ravines there is scrubby vegetation; I found no *pogus* on these ridges. Thus, this form is strikingly fragmented into demes and fulfills almost ideally the definition of "clumped" populations.

Once the proper, damp, shady, ravine habitats are entered, *A. w. pogus* is found in very large concentrations. I collected 26 specimens in an area of about 100 square meters at Colombier Valley, without making a discernible dent in the numbers around me. I took ten specimens from a 20 meter stretch of stone wall in the Grand

Fond, Quartier d'Orlean, and estimated I was collecting one out of every three seen. In the other localities—Loterie (French) and Cul-de-Sac (Dutch)—*pogus* was no less abundant. Although this form apparently has been severely curtailed in geographic range by human activities, it probably owes much of its present abundance in the areas where it survives directly to man: stone walls seem surely to be its ideal habitat.

In perch height, foraging habits, and retreat behavior, *A. w. pogus* is quite like other representatives of its species. The phrase "basically rupicolous" characterizes it well.

Distribution. So far as is known, presently confined to ravines in the interior uplands of St. Martin; previously, this form occurred on Anguilla and possibly (no evidence) on St. Barts.

Relationships. This is the most distinctive form of *Anolis wattsi*. It is regarded as a subspecies because *A. w. schwartzi*, of the St. Kitts Bank, shows character approach to it, concordant with geographical approach in three characters: increasing scale size, development of the neck band, and development of sexual dimorphism in head size (see *Relationships, A. w. schwartzi*, above). I regard its resemblance to *A. w. forresti*, principally in male throat fan color, as convergence accidentally resulting from two different sorts of selection pressures: character divergence from *Anolis gingivinus* in *pogus*, and open, arid ecology in *forresti* (see *Discussion*, below).

Assessment of the biological significance of the demonstrably larger scales of freshly collected *pogus* as compared to those of pre-1923 collected material would be simplified if I had more precise data on the older specimens (see *Squamation*, under this form, above). Three possibilities present themselves: (1) *A. w. pogus* were all smaller scaled forty years ago, and the whole subspecies has evolved towards larger scales; (2) the presently surviving populations had (as they now have) large scales forty years ago, and lowland populations, now extirpated, had smaller—or at least more variably sized—scales; (3) an average scale size difference existed between St. Martin and Anguilla populations, and that the older St. Martin example (MCZ 20986) is a chance sample from the overlap percentage of specimens. In any case, present *A. w. pogus* is different from its ancestors of only forty-five years back in two respects: it no longer occurs on Anguilla, and it has significantly larger scales.

I dismiss the possibility that the three older specimens bear faulty locality data because: (1) they were taken by two different collectors at two different localities; (2) evidence, in the form of tree stumps of large diameter, attests that *A. w. pogus* could have lived on Anguilla in the recent past; (3) what little pattern remains (mostly middorsally) indicates that in this respect these older specimens were *pogus*, and not one of the other forms; and, (4) they were all discovered in large series of *A. gingivinus*, the abundant species of the Anguilla Bank.

Discussion. Of all the races of *Anolis wattsi* described above, only *A. w. forresti* has been a center of nomenclatural confusion. Barbour (1923) described *forresti* on the basis of preserved specimens collected on Barbuda by W. R. Forrest. Barbour never saw living material, but the color characters he cites as distinguishing *forresti* are quite correct. Underwood (1959), unable to distinguish *forresti* and *wattsi* on the basis of preserved material, synonymized the former. Largely on the basis of the field notes taken by Auffenberg and King, Williams (1962a) described "*Anolis alter.*" I have been able to read these field notes in typescript form, revisit the collecting sites mentioned, and collect large series of fresh material from all over Barbuda. The Auffenberg-King field notes contain no actual misstatements of fact. However, four implications run through the relevant sections of these notes: (1) that the sinkholes, like Derby Cave, contain a distinctive plant association characterized by cabbage palm; (2) that the anoles in the sinkholes were observed to be distinct from those of the surrounding countryside; (3) that the anoles of the surrounding countryside were observed to be similar to *A. w. wattsi* from, for example, St. John's, Antigua; and, (4) that the anoles in the sinkholes were brightly colored ("red" and "green" are descriptive terms used frequently without modifying adjectives). Not one of these items is unequivocally stated, but all are implied; not one of these items is true. Occasional big trees and many dense clumps of cabbage palm (*Euterpe* sp.) are scattered all over the island of Barbuda. The same somber, pale, drab, little *Anolis wattsi* occurs all over Barbuda without a hint of geographic variation, and is not at all confined to palm clumps. All Barbuda *Anolis wattsi* are different from all Antiguan members of the species (though intermediates do occur in extreme northern Antigua and on the northeastern coastal cays). The specimen of "alter" collected by Auffenberg and King at Gaynor's Mill, in Antigua, has been darkened by strong formalin, but 17 better preserved specimens taken by three different collectors (nine collected by me) from this area are identical to typical specimens of nominate *wattsi*.

Auffenberg sent living specimens to Williams, and while he was somewhat disappointed by their lack of bright colors, Williams did not question the other implications in the story. The anoles from the sinkholes were clearly different from those in most of Antigua, and he named them anew.

Finally, Etheridge (1964) gave the range of *A. w. forresti* as Barbuda and Antigua (thus excluding nominate *wattsi* from its type locality). The simplicity of the real situation in no way merits the confusion that has accrued; I hope this confusion is herein laid to rest.

It is perhaps remarkable that a difference between *Anolis wattsi* on Antigua and Barbuda exists at all; the *Anolis bimaculatus* populations on these two islands (of the same bank) are not similarly differentiated. I can only suggest that Antigua and Barbuda are very different to a basically rupicolous anole; shade is permanently abundant on the former, more mesic, island, while shade on very xeric Barbuda is apt to be temporary, shifting, and very limited in extent. To the decidedly arboricolous *A. bimaculatus* representative, however, the two islands are similar. There are, of course, fewer trees on Barbuda (and fewer *bimaculatus* correspondingly), but the top of a Barbuda tree is in no way different from the top of an Antigua tree (from the lizard's viewpoint) once you have climbed up to it. In short, the conditions on the ground are generally different between the two islands, but the conditions in the trees are essentially the same; therefore, the anoles of the ground are different, while the anoles of the trees are the same. This explanation is, of course, pure speculation.

The differentiation of the other races of *A. wattsi* is less difficult to explain, perhaps, because one may appeal to geographic isolation. While Antigua and Barbuda were, presumably, part of a continuous land area during parts of the Pleistocene, the ranges of *A. w. schwartzi* (St. Kitts Bank) and *A. w. pogus* (Anguilla Bank) could never have been connected by land, either to each other or to the land areas of the Antigua Bank. Because Antiguan *wattsi* and St. Kitts Bank *schwartzi* are basically similar in coloration and pattern, their principal difference, scale size, might be entirely attributed to geographic isolation; there is certainly no evident selection pressure for, or adaptive value in, possessing smaller (or larger) scales, and no apparent linked or pleiotropic adaptive character.

A. w. pogus of St. Martin survives in habitats no more xeric than some in which *schwartzi* or nominate *wattsi* abound, and nowhere occurs in the very arid circumstances of *forresti*. Unless we postulate that *pogus* is directly derived from *forresti*, therefore, an ecological basis for the resemblance of these two forms is perhaps something of a puzzle. I suggested above that these resemblances (principally male throat fan color) are the result of convergence, and that other characters—such as scale size, neck banding, and sexual dimorphism in head size—indicate derivation of *pogus* from *schwartzi*. To reconcile the white throat fan of male *pogus*, and the lack of female flank stripe, with this view, I suggest character divergence between the sympatric species. The principal physical characteristic of male display in *A. b. bimaculatus* of the St. Kitts Bank is a huge nuchal crest; there is hardly any throat fan at all. Thus, perhaps, the large, bright throat fan of *schwartzi* has served as an excellent interspecies recognition character. In St. Martin, *A. gingivinus* has a small, but well-developed, prominently displayed, bright orange-yellow throat fan; *A. w. pogus* may have evolved a white throat fan as a response to selection pressure against interspecies confusion.

The same argument may be made for the presence or absence of the female flank stripe: *A. b. bimaculatus* has a rather vague anterior flank stripe; sympatric *A. w. schwartzi* has a distinct posterior flank stripe. *A. gingivinus* has a bold flank stripe from axilla to groin; sympatric *A. w. pogus* has no flank stripe at all. Similarly, character divergence reasoning may be applied to female middorsal pattern: vague in *bimaculatus*, bold in *gingivinus;* bold in *schwartzi*, very narrow and indistinct in *pogus*. In the field, *A. gingivinus* (with prominent flank and middorsal stripes) gives the impression of a longitudinally striped lizard; *A. w. pogus* possesses striking vertical bars.

Anolis wattsi, as a species, may have been derived directly from the very similar *Anolis acutus* of St. Croix. If this supposition is made, then either nominate *wattsi* of Antigua or *schwartzi* of the St. Kitts Bank seems closer to the ancestral stock than are *forresti* or *pogus*. Niche segregation seems far better developed between *Anolis bimaculatus leachi* of the Antigua Bank and the two *wattsi* forms there than it is between *A. b. bimaculatus* of the St. Kitts Bank and *A. w. schwartzi*. Further, Antigua Bank *wattsi* has abundantly occupied all of the available land areas on its bank, and has differentiated into two geographic races. *A. w. schwartzi* appears unable to inhabit much of the more xeric and open land area of the St. Kitts Bank, and shows only the slightest geographic variation through three islands. All this suggests *A. w. wattsi* as the oldest established and closest of the ancestral form.

Conversely, *A. w. schwartzi* is closest to *A. acutus* in squamation (the only one of the *wattsi* complex that impinges in ventral count), and geographically more proximate to *acutus* than is nominate *wattsi*. Too, though niche segregation is poorly developed in the lowlands of the St. Kitts Bank, all of these islands provide ecological zonation, and *schwartzi* and *bimaculatus* may well have originally evolved an ecological division of the available land areas on a geographic basis. *A. b. leachi* and *A. w. wattsi* lacked the possibility of such a solution to the sympatry problem, because their land areas lacked ecological zonation; vertical niche segregation throughout their ranges was an alternative. Character divergence (especially the male throat fan) is far more pronounced between *schwartzi* and nominate *bimaculatus* than between nominate *wattsi* and *leachi*. I personally find the arguments for *schwartzi* as the original *wattsi* stock (squamation, geographic proximity, and degree of character divergence) more convincing than those for nominate *wattsi*.

My proposed speculative evolutionary history of *Anolis wattsi* is, therefore, as follows: *A. acutus* stock arrived in the St. Kitts Bank from St. Croix, and there diverged into the form we know as *A. wattsi* today. Antigua was colonized from the St. Kitts Bank stock and diverged into *A. w. wattsi;* at this time *A. wattsi* of the St. Kitts Bank was developing into the present race *schwartzi.* Barbuda was colonized directly from Antigua, and ecological selection pressures (open, arid) differentiated *A. w. forresti.* The Anguilla Bank was directly colonized over water from the northern end of the St. Kitts Bank (St. Eustatius today) and *A. w. pogus* has developed in response to selection pressures for character divergence from *A. gingivinus.*

Of course, quite a different reasoning could be argued: *Anolis wattsi,* as we see it now, could be the result of waves of invasion from the west. *A. w. schwartzi* is the most similar to *A. acutus* in coloration and squamation combined, and thus the most recent arrival. This argument would imply, however, that *pogus* is the oldest (seemingly most different from *acutus*), and this might involve asserting that white throat fan, lack of flank stripe, and large scales are primitive. The first two might be rejected as character divergence, but the last is difficult to dismiss. All are contradicted as primitive by the evidence of bright (usually yellow) throat fans, flank stripes, and medium to small scales in *Anolis acutus* and the vast majority of other Lesser Antillean anoles of the *bimaculatus* group. Too, this implies independent acquisition, in each wave, of the *wattsi* karyotype (see *Relationships, Anolis acutus*).

All of this leads to the question of which came first, the *bimaculatus-gingivinus* stock, or the *wattsi* stock? Underwood (1959), not knowing of differentiation within *wattsi,* regarded it as the recent invader. The present arrangement of three forms (*bimaculatus, leachi,* and *gingivinus*) in two species (*bimaculatus* and *gingivinus*) on the one hand, and four forms (*wattsi, schwartzi, forresti,* and *pogus*) in one species on the other, destroys the clarity of Underwood's argument. However, the development of jaw sculpturing (see Etheridge, 1964), giant size, and the reduction of the throat fan in *A. b. bimaculatus* and *A. b. leachi* would seem to be more major divergences from the postulated ancestral condition than any changes visible in the *wattsi* representatives (scale size and color). Seemingly, *A. wattsi* must have colonized the Anguilla Bank after *A. gingivinus* was established there, for the burden of character divergence logically falls on the incoming—rather than the entrenched—form. If *gingivinus* resembles the ancestral condition (bright fan color, flank stripe, small scale size, and generalized, ubiquitous habits) and was widespread and abundant throughout the Anguilla Bank (as it certainly is today) then *A. wattsi* arriving as a waif propagule over water would have had to make radical shifts in characters to survive. The fact that Anguilla Bank *wattsi* has diverged from both its sympatric and its dichopatric relatives within the past four decades corroborates this view.

Etheridge (1964) has shown the existence of *wattsi* on Barbuda in the Pleistocene; *A. bimaculatus* was also present at that time on Barbuda, and had reached the level of differentiation it shows today in osteological characters at least. Assuming that evolutionary rates, at least in osteological features, are roughly comparable in Lesser Antillean *bimaculatus* group anoles (though there is no evidence that this is true), Etheridge's facts tend to support the view that *bimaculatus* was established (at least on Barbuda) before the *wattsi* stock arrived.

The relationships of *A. sabanus* are discussed under that form. It need only be said here that the similarities of *wattsi* and *sabanus* in size, habitat, behavior, and the manner in which sexual dimorphism is expressed do not permit as quick dismissal of close relationship as some of the obvious distinctions in squamation might suggest.

Anolis sabanus Garman

Anolis sabanus Garman (1887: 39)

Type. MCZ 6161, Lagois coll. The large male bearing the tag is here designated lectotype; five other untagged males are included in the present series.

Type locality. "Saba." As this species occurs nowhere but on this small island, and shows but minimal geographic variation, further restriction of the type locality seems unnecessary.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening 2.3 or more times; no orange or red on orbital area; dark spots present.

Squamation. Eighty-three specimens (57 males and 26 females) are similar to other Lesser Antillean members of the *bimaculatus* group except in the following characters: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are quite smooth; there are 19–24 (average 22) in the standard distance at midbody. The middorsals average smaller than the ventrals in females (24–33, average 28, in the standard distance) but about the same size in males (19–25, average 22); the middorsals of males are frequently somewhat subimbricate, those of females are not. The scales lateral to the middorsals grade abruptly in males, and gradually in females, into smaller dorsal granules; in both sexes there are 30–40 (average 35) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital pads are well developed and clearly of the "raised" type of Boulenger (1885) and Williams (1963) in males, but reduced in females. Males have 24–28 (average 26), females but 21–25 (average 23) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. This is the harlequin of Lesser Antillean anoles. Males vary from ash grey with a green cast to *café-au-lait* brown in ground color; large sooty black or slate blue spots crowd the dorsal surfaces. The orbital area is paler than the ground color, and is often blue-grey. A short vestige of a flank stripe is usually greyer or bluer than the ground color in the axilla, and frequently accentuated by coalescing spots above and below. Sometimes a number of large dorsal spots coalesce to form striking, broad stripes; MCZ 85573, from St. John's, is extreme in this respect. The ventral surfaces are light greenish yellow. The throat fan is light, bright greenish yellow shading toward orange-yellow at the anterior center. The fan scales do not contrast to their ground color, except in the most orange-yellow portion of the fan.

Females are generally paler than males, varying from grey or olive to light brown; their spots are reduced to mottlings and smudges, but still quite visible. A mottled, ladder, or sometimes striped middorsal pattern is indicated. The vague flank stripe is often better developed than in the male, and extends over the shoulder. The greenish yellow belly frequently has a metallic sheen.

Color change, to lighter or darker, is weakly developed in both sexes.

There is a definite cline in color from xeric coast (e. g., Flat Point) to the crater of The Mountain. At Flat Point (MCZ 75524–8) specimens show little yellow, tending toward grey or grey-green ventrally; above Little Rendezvous, at *ca.* 700 m (MCZ 75539–43), all specimens had a green cast, and one female (MCZ 75541) was described as olive all over with "rather bright green sides." Similarly, all three females from this elevation (MCZ 75541–3) had a coppery tinge to the head; this was occasional at The Windward Side and The Bottom, but was not found among three females taken at Flat Point (MCZ 75526–8).

Patterns of adult *A. sabanus* are shown on Plate 1.

Size and sexual dimorphism. Males of *Anolis sabanus* attain 69 mm snout-vent length (MCZ 6161, type); females reach 50 mm (MCZ 28521). The smallest males examined appeared sexually mature (MCZ 75540, from The Mountain above Little Rendezvous, and an untagged specimen with MCZ 28501, etc.) and are 44 mm snout-vent length. The smallest female examined (MCZ 75543, The Mountain above Little Rendezvous) is mature at 42 mm. Thus, adult sizes overlap considerably.

The considerable sexual dimorphism in color not withstanding, it is in squamation that *A. sabanus* is extreme. With respect to both middorsals and subdigital lamellae the sexes of this species are more different from each other in squamation than are several other pairs of forms (e. g., *bimaculatus* and *nubilus*) that I regard as full species. Males have strikingly larger middorsals and more lamellae than do females (see above).

The standard distance is 17–19 (average 18) per cent of the snout-vent length in both sexes; thus the middorsal scale size dimorphism is real, and not a result of proportional differences.

Population structure and ecology. Anolis sabanus is infradispersed and abundant all over Saba except in the driest areas. At Flat Point, for example, I found specimens decidedly clumped around the few bushes that provided shade. In behavior this species is far from ubiquitous; a peculiar fact, since it is the only *Anolis* on the island. *A. sabanus* stays close to the ground; males may perch as high as five feet, but females and young seldom go above three feet. Retreat behavior is usually either down or laterally into cavities and crevices. This species likes to remain pressed flat against a vertical substrate, and keeps the forelimbs more extended than is normal for other anoles. Males even display from this position: simply lifting the head at an angle before extending the very large throat fan. Barbour (1930a, 1935) was quite correct in asserting that *sabanus* is a basically rupicolous form; in fact, this species gives the most strongly geckolike impression of any in the Lesser Antilles.

Distribution. Anolis sabanus is confined to Saba, where it occurs from sea level to the top of The Mountain (870 m). The species does not occur on either the Diamond Rock or Green Island; the latter cay is thus the only bit of land I have encountered in the Antilles that has shrubs (two) but lacks *Anolis.*

Relationships. Barbour (1930a, 1935) argued cogently for a close relationship between *sabanus, wattsi,* and *acutus;* habitat and behavior amalgamate the first two, morphology bonds the second to the last. Then, Barbour (1937) turned around and confounded *acutus, wattsi,* and *forresti,* along with *Anolis gingivinus,* under the unrelated *A. krugi* of Puerto Rico. It is little wonder that Underwood (1959) believed none of Barbour's ramblings, and dumped this remarkable little species into his catch-all *Anolis bimaculatus.*

Anolis sabanus is probably the most immediately distinctive Lesser Antillean anole. Even pickled females show the dark spots that set them strikingly apart. The behavior of the species is bizarre. One cannot put characters like the manner in which sexual dimorphism is expressed into keys or diagnoses, but surely the dimorphic squamation of this species argues strongly for a long and independent evolution.

In the end, Barbour's initial view seems basically correct. *Anolis sabanus,* with its standard *wattsi*-type karyotype, is probably an immediate derivative of first *acutus*-type stock colonizing islands east of St. Croix; that stock has subsequently given rise to *wattsi* and the remainder of the *bimaculatus* group in the northern Lesser Antilles. The resemblances between *sabanus* and *wattsi* thus appear as holdovers from their common past; the differences between *sabanus* and its other relatives reflect its long isolation.

Anolis gingivinus Cope

Anolis gingivinus Cope (1864: 170)
Anolis virgatus Garman (1887: 41)

Type. BMNH 1946.8.29.18–20 (*fide* Underwood, 1959), W. J. Cooper coll.

Type locality. "Anguilla rock nr. Trinidad," here restricted to Sandy Ground, Anguilla.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior border of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening less than 2.2 times; subdigital lamellae 17–24.

Squamation. One hundred seventy-five specimens (111 males, 61 females, and 3 juveniles) are similar to other Lesser Antillean *bimaculatus* group anoles except in the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; there are 19–26 (average 22) in the standard distance at midbody. The middorsals average smaller than the midventrals; there are 20–29 (average 26) contained in the standard distance; the middorsals are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly into smaller dorsal granules; there are 39–50 (average 45) of these in the standard distance six scale rows lateral to the dorsal midline. The digital pads are broad and of the "raised" type. There are 17–24 (average 20) lamellae under the second and third phalanges of the fourth toe.

Coloration. In life, *Anolis gingivinus* varies from the usual olive drab to distinctly light greenish, or even rusty, in ground color. The venter varies from cream to bright yellow. The throat fan of males is well developed and yellow-orange in color, with white scales. Color change is merely to darker, enhancing the grey-brown pattern; greener individuals turn browner. The pattern consists basically of a very broad middorsal band, which may be lighter or darker than the ground color in the same individual at different times, and a bold, light flank stripe from shoulder to groin. In males, this pattern is often modified by the inclusion of spots or marbles of grey-brown. (Lazell, 1964c: 717.)

There is something of a geographic element in variation in this species, resulting, I believe, from the deme structure imposed by spreading its range over at least forty islands, cays, and rocks from Sombrero, throughout the Anguilla Bank, to the Ile Coco. Virtually every variant observed in *A. gingivinus* can, however, be found in a single population like that at Phillipsburg, St. Martin, or The Valley, Anguilla. Here are some of the extremes I noted elsewhere: palest and greyest, Scrub Island; brightest yellow bellies: Lower (= western) Prickly Pear Cay; brightest orange fans, Dog Island; palest yellow fans, Sombrero and Scrub Island; darkest and most uniform, Ile Coco; most regular oval spotting, Sombrero and Ile Tintamarre (= "Flat Island"); reddest, Guana Cay of Pelikan and Ile Coco.

Adults of both sexes are shown on Plate 1.

Size and sexual dimorphism. The largest male of *Anolis gingivinus* is 72 mm, snout to vent (MCZ 75603), and comes from Guana Cay of Pelikan; a female (MCZ 75605) from the same tiny islet holds the record for her sex: 53 mm. The distant Ile Coco supports a population that comes in a close second: a male 68 mm (MCZ 75630), and a female 51 mm (MCZ 75634). Elsewhere in its range, *A. gingivinus* rarely exceeds 65 mm and 48 mm, for males and females, respectively. The smallest apparently mature male is 42 mm (MCZ 75552, Sandy Ground, Anguilla),

PLATE 1

1. *Anolis acutus*: male, JDL 36; female, JDL 42; Christiansted, St. Croix.
2. *Anolis sabanus*: male, MCZ 75530; female, MCZ 75537; The Bottom, Saba.
3. *Anolis gingivinus*: male, MCZ 75544, Sandy Ground; female, MCZ 75555; The Valley, Anguilla.
4. *Anolis nubilus*: male, MCZ 82934; female, MCZ 82942; Redonda.
5. *Anolis wattsi wattsi*: male, MCZ 75635; female, MCZ 75641; St. John's, Antigua.
6. *Anolis wattsi forresti*: male, MCZ 75724; female, MCZ 75730; Codrington, Barbuda.
7. *Anolis wattsi schwartzi*: male, JDL 209 (Type); female, JDL 214; Nevis Peak.
8. *Anolis wattsi pogus*: male, JDL 100 (Type) shown in extreme color changes; female, JDL 107; Colombier Valley, St. Martin.

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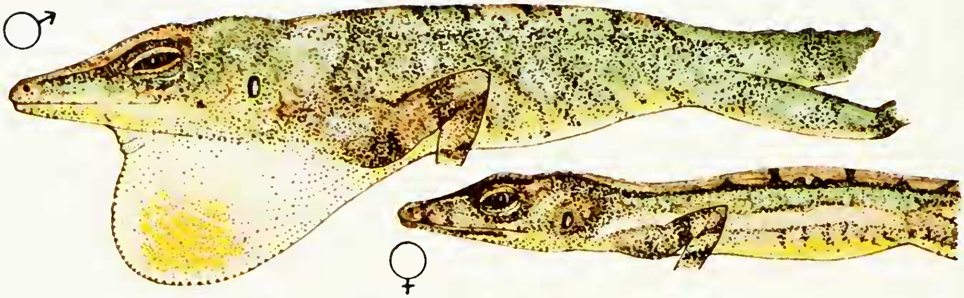
1



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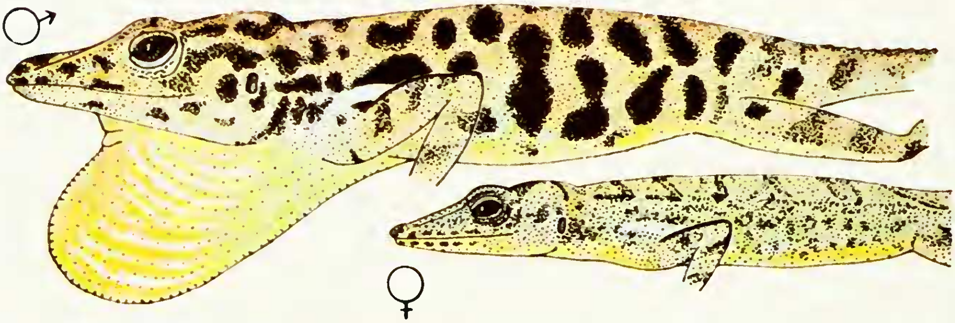

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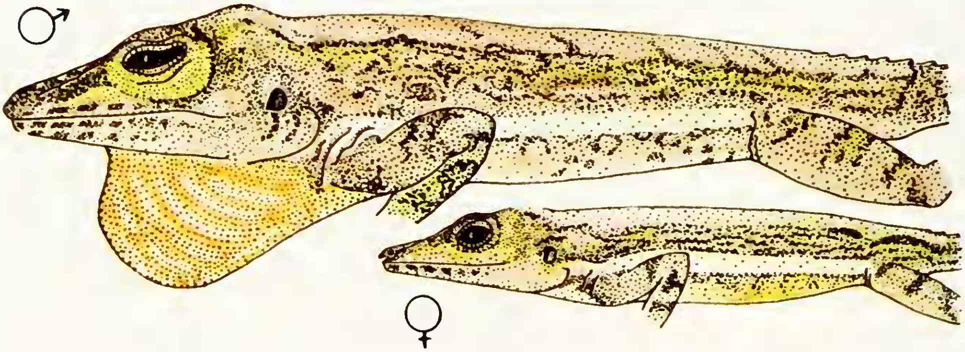

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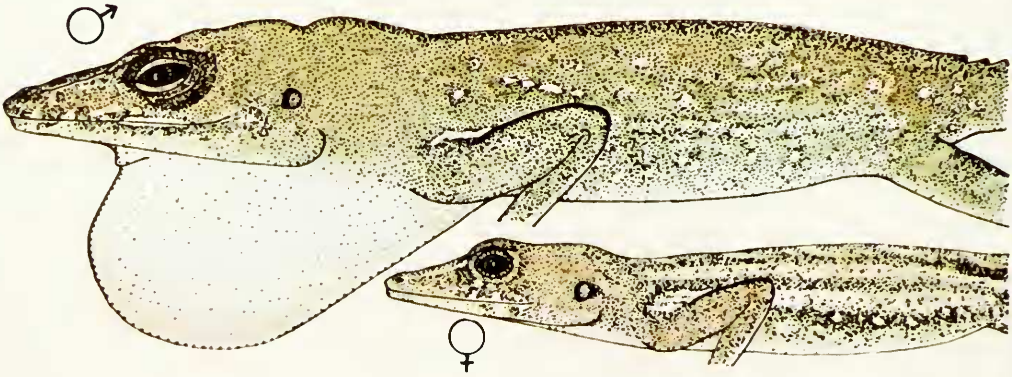

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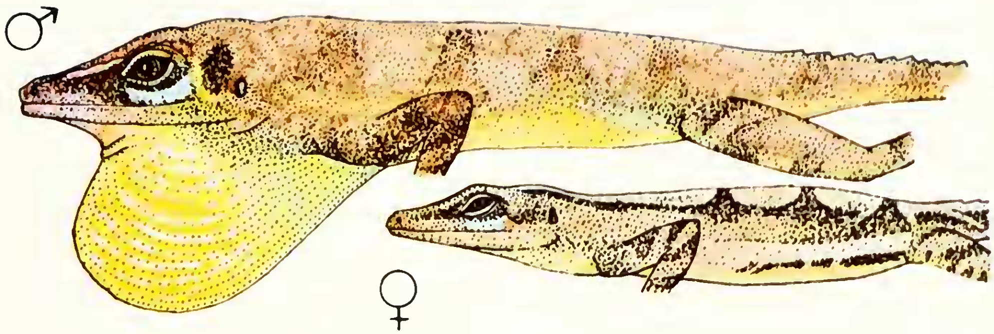

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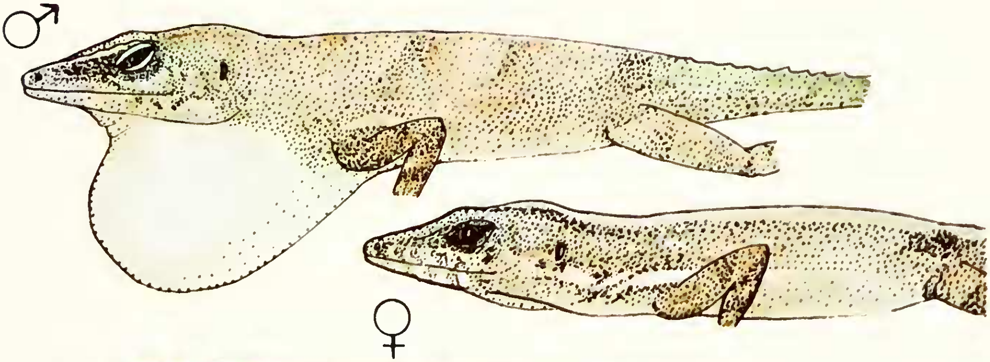

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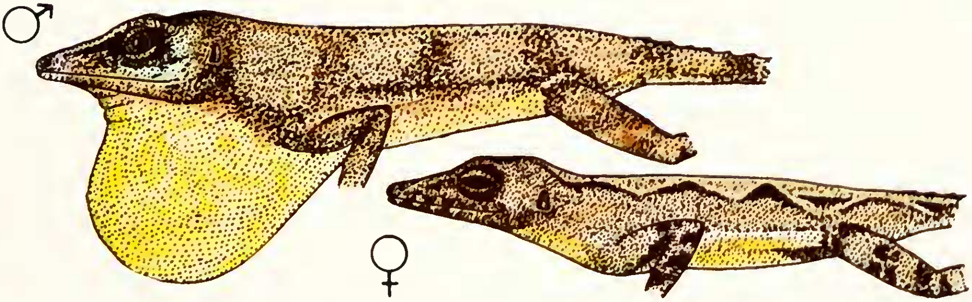

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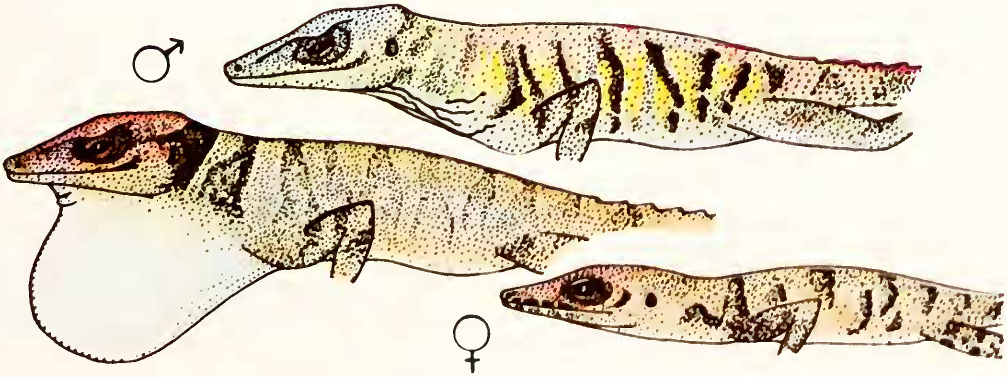

and the smallest mature female is 41 mm (MCZ 75555, The Valley, Anguilla). The fact that Guana Cay and Ile Coco have such large individuals and also agree in averaging more reddish than most other populations is interesting. The two islets are both small, but not otherwise especially similar: Guana Cay is high and steep, with but three or four small bushes; the Ile Coco is a low, flat, honeycombed limestone platform with patches of dense brush. Guana Cay is just south of St. Martin, and about twenty miles northwest of the Ile Coco; Guana Cay is about in the middle of Anguilla Bank, while the Ile Coco is its southern terrestrial terminus. I suggest that perhaps redness and large size are pleiotropic effects of the same gene, and that this gene has been independently acquired by founding populations, or coincidentally retained in stranded populations, on these two islets.

The sexes of *A. gingivinus* are remarkably similar; no sexual dimorphism is evident in squamation, and the standard distance is 17–21 (average 19) per cent of the snout-vent length in both sexes. In coloration and pattern the sexes are quite similar, except for the somewhat more complex markings and throat fan of the male. The tendency for females to have brighter yellow bellies than males is interesting; this feature may be a holdover from the presumably not distant *A. acutus* stock, which also possesses it. There is considerable overlap in adult sizes.

Population structure and ecology. As I have discussed this species elsewhere (Lazell, 1964c), it suffices here to say that *A. gingivinus* is ubiquitous in habits, quite like *A. acutus.* Even where it occurs with *A. w. pogus,* the species is abundant, and the two intermingle spacially and territorially at the rupicolous end of the *gingivinus* niche. *A. gingivinus* is infradispersed throughout the land areas it occupies, but, as I noted above, the fragmentation of its range into forty or more separate islands imposes a clumped deme structure upon it, from an evolutionary point of view.

Distribution. Anolis gingivinus occurs throughout the Anguilla Bank, on every rock and cay that supports more than herb-stage vegetation, and on Sombrero.

Relationships. In size, behavior, and the expression of sexual dimorphism, *Anolis gingivinus* is strikingly like *Anolis acutus.* The smooth ventrals, however, suggest *sabanus* or *bimaculatus.* The midventrals average larger than the middorsals; this is true of *sabanus,* if both sexes are amalgamated, but the opposite of the condition in either *acutus* or *bimaculatus.* A number of more subtle features, however, suggest proximity to *bimaculatus:* the stocky build; the prominent subotic bulge of adult males; the comparatively small throat fan; and, the presence of slight jaw sculpture in the largest males (e. g., MCZ 75603, discussed above). If I speculate that all of these features, as well as increased size and number of subdigital lamellae, are specializations of the *bimaculatus* stock over the original post-*acutus,* pre-*wattsi* stock that initially settled east of St. Croix, then *A. gingivinus* may be seen as an intermediate between these two stocks. That is, *gingivinus* may well be a product of the original post-*acutus* radiation that gave rise to pro-*wattsi* (on the St. Kitts Bank) and *sabanus* (on Saba); pro-*bimaculatus,* then, would be a derivative of *gingivinus,* originally on the Antigua Bank.

If the above speculative arrangement was correct, one might hope to find a population elsewhere that signalled the advance from *gingivinus* to pro-*bimaculatus,* but had avoided some of the extreme modifications of present-day *bimaculatus* that result from character divergence in sympatry with *Anolis wattsi.* Just such a form does, in fact, occur: *Anolis nubilus* of Redonda. *A. nubilus* is remarkably similar to *A. gingivinus,* and differs from it principally in ways (like number of subdigital lamellae) that indicate a shift toward *bimaculatus* (see *Relationships* under *A. nubilus*, below).

Anolis bimaculatus (Sparrmann)

Lacerta bimaculata Sparrmann (1784: 169)

Type. A specimen in the Museum de Geer Royal, Stockholm, *fide* Underwood (1959).

Type locality. St. Eustatius; no restriction seems necessary.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening less than 2.2 times; subdigital lamellae 26–36; male with small throat fan entirely, or marbled with, yellow or orange; female without bold whitish spots or streak over hind limb insertion.

Remarks. Anolis bimaculatus is the giant of its group, with males of both subspecies frequently exceeding 110 mm, snout to vent. There is considerable geographic variation in apparent size and color within each of the subspecies, and the two seem to be diverging from each other in ways—like jaw sculpture, nuchal crest, and throat fan—that are of major evolutionary import. Nevertheless, I can find no character or combination of characters that will invariably separate the two forms, and thus retain them as conspecific. Geographically, these forms are simple: *A. b. bimaculatus* occurs on the islands of the St. Kitts Bank; *A. b. leachi* occurs on the islands of the Antigua Bank and has been introduced into Bermuda.

Anolis bimaculatus bimaculatus (Sparrmann)

Lacerta bimaculata Sparrmann (1784: 169)
Anolis edwardsi Merrem (1820: 45)
Anolis reticulatus Gray (1840: 114)
Anolis mayeri Fowler (1918: 8)

Type. A specimen in the Museum de Geer Royal, Stockholm, *fide* Underwood (1959).

Type locality. St. Eustatius.

Diagnosis. An *Anolis bimaculatus* with a green orbital region; spots, when present, frequently dominated by a large dark costal one on each side; male throat fan very small, extensible nuchal crest very large.

Squamation. One hundred ninety-seven specimens (113 males, 77 females, and 7 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group except in the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; there are 21–32 (average 26) contained in the standard distance at midbody. The middorsals average larger than the midventrals; there are 21–27 (average 23) in the standard distance; the middorsals are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to smaller dorsal granules; there are 29–37 (average 33) in the standard distance six scales lateral to the dorsal midline. The digital pads are broad and raised; there are 26–35 (average 30) subdigital lamellae under the second and third phalanges of the fourth toe. I found no significant differences in squamation between the populations of this form on St. Eustatius (45 examined: 29 males, 15 females, 1 juvenile), St. Kitts (109 examined: 59 males, 46 females, 4 juveniles), and Nevis (43 examined: 25 males, 16 females, 2 juveniles).

Coloration. This is a basically green anole with green orbital skin; beyond those facts, it is an extremely variable species, and virtually the full range of variation may be seen in the St. Kitts population. Cochran (see Williams, 1962a: 457) describes a specimen near the gaudy extreme, but apparently lacking the ornate black and grey or brown trunk-spotting so frequent in this species. MCZ 75472, collected by me in Basseterre, showed the shades of pink, orange, yellow, green, and blue mentioned by Cochran, and had a large, sooty costal spot, and mottlings of grey-brown bordered black on the dorsal surfaces. MCZ 75464, collected by me at Willet's Estate, was virtually uniform green, shading to yellowish on the throat and white on the venter. There were no dark spots. MCZ 75469, collected by me at Basseterre (Fig. 22), is a near rival to this extreme. Most individuals of either sex, anywhere in the range of this subspecies, show at least the dark costal spot.

The notes quoted by Williams (1962a: 456–458) intimate the possibility of inter-island differences. Anxious to document such predictable (owing to isolation) differences, I paid very careful attention to colors and patterns in the field. The entire St. Eustatius population is much less variable than either of the larger island populations, and near the spotted and mottled extreme noted for MCZ 75472 above; all St. Eustatius specimens, however, are completely included within the range of Kittitian variation. The consensus, reported by Williams, that Nevis specimens are less spotted (or have the costal spot less distinct) is sharply contradicted by my specimens and observations: JDL 229, taken at Market Shop, is as spectacularly spotted as any animal of any species known to me; it has no more spots than, for example, MCZ 75472 from St. Kitts, and lacks the transverse mottling common to what I regard as the most patterned extreme; it has, however, very sharp definition of about 40 ink-black dots on each side of the head and body, about two dozen on the dorsal surfaces of the hind limbs, and even some on the forelimbs; the costal spot is one of the biggest and boldest: about half again the size of the ear. On the very next tree I collected JDL 230, a specimen with hardly any dorsal spotting at all, and quite without a costal spot; JDL 230 had as brilliant yellow a shoulder stripe, however, as I have seen (cf. King *in* Williams, 1962a: 457). In summation, then, *Anolis bimaculatus bimaculatus* is an exceedingly individually variable form, and no way of distinguishing specimens from the three islands on the basis of color can be found.

The ventral surfaces of this form vary from light green or yellow to white. The tiny throat fan of males is rarely used and highly variable: it may be all yellow or orange, or spotted or streaked with orange or yellow on a whitish ground; the scales may conform to the ground color, or be creamy to dull white. Females are so similar to males as to be quite inseparable on color characters when like-sized specimens are compared; they never attain the gaudy hues and bold markings that some old males achieve, however.

Color change from the normal green condition is to chocolate or blackish brown when upset. Color patterns of both sexes are shown on Plate 2.

Size and sexual dimorphism. The largest male examined is 114 mm, snout to vent (MCZ 75469), and comes from Basseterre, St. Kitts. The smallest apparently mature male is 62 mm (MCZ 75446), from Boven Bay, St. Eustatius. The largest female examined is 69 mm (MCZ 75473) from Basseterre; the smallest mature female is 52 mm (MCZ 75335) from Gilboa Hill, St. Eustatius. Because important inter-island size differences have been suggested to me by several people in conversation, and seem indicated by King's comments (*in* Williams, 1962a: 457), a closer scrutiny of the question is in order:

On St. Eustatius, 29 mature males range from 90 to 62 mm, snout to vent (MCZ 75325, Oranjestad, and MCZ 75446, Boven's Bay, respectively); 15 mature females range from 67 to 52 mm (MCZ 75319, Oranjestad, and MCZ 75335, Gilboa Hill, respectively).

On St. Kitts, 59 mature males range from 114 to 63 mm (MCZ 75469, Basseterre, and MCZ 65294, Golden Rock Airport, respectively); 46 mature females range from 69 to 54 mm (MCZ 75473, Basseterre, and JDL 167, 2.5 miles northeast of Lambert's Estate Yard, respectively).

On Nevis, 25 mature males range from 112 to 63 mm (JDL 230, Market Shop, and JDL 193, Charlestown, respectively); 16 mature females range from 66 to 53 mm (MCZ 28714, "Nevis," and MCZ 65290, Newcastle, respectively).

Therefore, no significant differences exist between the three island populations in minimum male size (62, 63, 63), maximum female size (67, 69, 66), or minimum female size (52, 54, 53). The only significant difference is in maximum male size between St. Eustatius (90) and St. Kitts-Nevis combined (114 and 112). On St. Eustatius a colubrid snake of the genus *Alsophis,* a presumed lizard eater, is prevalent; this snake does not occur on either St. Kitts or Nevis. Bearing in mind my remarks on "giant" (i..e., 100 mm plus) anoles made above (under "the genus *Anolis*"), it is possible to interpret the difference in maximum male sizes attained as a result of predation, and not as an indication of genetic differences between populations.

The sexes of *A. b. bimaculatus* overlap little in size at maturity, but are otherwise quite alike, barring the obvious distinction of the postanal plates in males.

The standard distance is 17–20 (average 18) per cent of the snout-vent length in both sexes.

Population structure and ecology. This species is abundant and infradispersed throughout the lowlands of all three islands; at high elevations it is absent, though I have taken a specimen at 1100 feet (JDL 167, forest edge, southeast rim of Godwin's Gut, 2.5 miles northeast Lambert's Estate Yard), and seen several others at the same locality. Clearing forest will presumably extend the range of this species altitudinally, if it is permitted to occur. *A. b. bimaculatus* is quite ubiquitous in habits, despite its large size and such seemingly arboreal adaptations as high lamellae counts. Males may perch as high as ten to fifteen feet above ground, but are usually at about three to six feet; they commonly forage with females and juveniles on the ground, and thus, frequently, with *Anolis wattsi schwartzi* (see "*Popultaion structure and ecology*" of that subspecies, and the general "*Discussion*" of *Anolis wattsi*). Whenever *A. w. schwartzi* occurs in the lowlands, the two species interact. Males frequently display at each other, and the very large fan of tiny *schwartzi* sometimes seems to deeply impress the virtually fanless, giant *bimaculatus.* I suspect that, originally, *A. b. bimaculatus* was far less abundant and widespread than it is today; an almost completely parapatric situation may have existed between the two species, with *bimaculatus* confined to open, arid areas and littoral, and *schwartzi* confined to shady woods. Clearing the forest for agriculture made possible a *bimaculatus* expansion into *schwartzi* territory; perhaps the two species, once largely geographically separated by ecological zonation on these high, first cycle islands, interact so vigorously today simply because they have not yet adapted to large-scale sympatry.

Distribution. Anolis bimaculatus bimaculatus occurs throughout St. Eustatius, St. Kitts, and Nevis, in open, sunny areas to at least 1100 feet elevation.

Relationships. This form differs significantly from *A. b. leachi* in the following respects: the nuchal crest is much more developed, and is extended to constitute the principal feature of male display; correspondingly, the throat fan is reduced to the minimum seen in any Lesser Antillean *Anolis,* and is considerably smaller (rather subjectively judged) than in *leachi;* jaw sculpture (noted by Etheridge, 1964) is much weaker in specimens of this form than in like-sized *leachi;* the costal spot is generally far more evident, and general vermiculation far less prevalent, in this form; the orbit is green rather than yellow. The last character is the best for separating all specimens, but the existence of *leachi* with decidedly yellow-green orbital skin (e. g., MCZ 75781, St. John's) leaves me no choice but to regard these two forms as still conspecific.

The relationships of the species are discussed under the following form.

Anolis bimaculatus leachi Duméril and Bibron

Anolis leachi Duméril and Bibron (1837: 153)
Anolis antiguae Barbour (1915: 74)
Anolis barbudensis Barbour (1923: 4)

Type. MNHN Ig. 34/1; T. Bell *leg.*, *fide* Underwood (1959).

Type locality. "Antilles," here restricted to St. John's, Antigua, capitol of the principal island on which the form occurs, and where it is abundant.

Diagnosis. An *Anolis bimaculatus* with predominantly yellow orbital skin; speckles or vermiculation on anterior trunk; usually not a large, dark costal spot on each side; male throat fan small, but well developed; extensible nuchal crest large, but not remarkably so.

Squamation. Ninety-five specimens (47 males, 41 females, and 7 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth (faint keeling may appear on some lateral ventrals; cf. Williams, 1962: 458); there are 20–30 (average 25) contained in the standard distance at midbody. The middorsals average slightly smaller than the midventrals: 21–32 (average 27) are contained in the standard distance; they are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to smaller dorsal granules; 29–38 (average 34) granules are contained in the standard distance six scales lateral to the dorsal midline. The digital pad is the largest and most strikingly "raised" of *bimaculatus* group anoles; there are 28–36 (average 33) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. The ground color of males varies from drab grey-green to brilliant yellow-green or blue-green; females from the drier parts of the range may be grey or grey-brown, without green. The orbital skin is basically yellow: sometimes quite bright, sometimes smudged with grey, and rarely light yellow-green. Grey to grey-brown vermiculation or small spots cover the anterior trunk and, usually, the head; females usually have a middorsal band relatively free of this dark marking. The ventral surfaces vary from light green or yellow to dull greyish white. The small throat fan of the male is yellow-orange to dull orange; the scales are usually paler than the skin, and frequently nearly white.

The full range of ground color variation may be seen at a number of localities: the north coast of Antigua (e. g., MCZ 57776–7, Hodge's Bay), or on Green Island, east of Antigua (MCZ 82108–9). The dullest individuals come from the most xeric regions: Barbuda (MCZ 75779–80, Codrington), Long Island, northeast of Antigua (MCZ 75783–4), and York Island, southeast of Antigua (MCZ 82110–5). Specimens from St. John's (e. g., MCZ 75781–2) may be as bright as any, or rather dull; I have a note dated 18.v.63 that all *A. b. leachi* seen at Body Ponds, northwest of Sweets Village, in the wettest part of interior Antigua, are very deep green with blue tones.

Several people (of admittedly ornithological leanings) have suggested that the name "*barbudensis*" Barbour (1923) is valid because less than 25 per cent of the Antiguan *leachi* population is as dull, or duller, in ground color as are all Barbudan specimens. That is to say, that if one were given a representative sample of *leachi* from all over its range, and picked the dullest individuals as "*barbudensis*," one would be right (i. e., they would be Barbuda specimens) 75 per cent, or more, of the time. If, however, one were given a series from, for example, Hodge's Bay, and one guessed the dullest specimens to be "*barbudensis*," one would be dead wrong

100 per cent of the time. The Barbuda type of *leachi* coloration is completely included within the Antiguan extremes of variation; Amadon (1949) and Mayr, Linsley, and Usinger (1953: 100) are perfectly clear on the point that this situation does not fit the 75 per cent rule for subspecies recognition. This situation in *A. b. leachi* may be instructively compared to the situation obtaining between *A. w. wattsi* (Antigua) and *A. w. forresti* (Barbuda): nominate *wattsi*, in the northern part of its range, sometimes approaches the diagnostic characteristics of Barbudan *A. w. forresti*; it never equals them.

Color change is from the normal green or grey to chocolate or blackish brown when upset. Color patterns of both sexes are shown on Plate 2.

Size and sexual dimorphism. The largest male *Anolis bimaculatus leachi* measured is 113 mm, snout to vent (MCZ 75779), from Codrington, Barbuda. That specimen was preserved 6.v.63, and the measurement was made 22.iii.65—after I had read Etheridge's (1964) account of the fossils from Barbuda; an 8 per cent shrinkage (see "Materials, Methods, Terms, and Concepts," above) would put this individual over 120 mm in life. Marks made in my field catalogue at snout tip and vent of the fresh dead animal are 123 mm apart; I regard this subspecies as the largest of all the *bimaculatus* group forms, and it certainly attains lengths today far in excess of that noted as maximal by Etheridge (1964). The following specimens may be noted for large size, as preserved: MCZ 16167, Barbuda ("*barbudensis*" type): 107 mm; MCZ 75783, Long Island northeast of Antigua: 109 mm; and, MCZ 75781, St. John's, Antigua: 111 mm. I can say with assurance that the two larger size classes of Barbudan fossils, which Etheridge regarded as representing two species, represent solely *Anolis bimaculatus leachi* (see remarks on "giant" anoles, under "The genus *Anolis*," above).

The smallest apparently mature males examined are both 68 mm, snout to vent (MCZ 65313–4), and are from Fort James, Antigua. The largest female examined is 70 mm (MCZ 66363), from Bermuda; a 69 mm specimen (MCZ 65306) is from St. John's Antigua. The smallest apparently mature female examined is 52 mm (MCZ 65311), from Fort James. Sexual dimorphism is not apparent in scales or proportions (standard distance 17–20, average 18, per cent of snout-vent length in both sexes), and very weakly indicated in color. With respect to size, however, dimorphism is quite sharp.

Population structure and ecology. This is an arboreal species: as close to a true crown dwelling form as occurs in the Lesser Antilles. Females and juveniles may rarely be encountered foraging on the ground, adult males virtually never. Perch heights for males vary from eight feet to as high as trees grow on the Antigua Bank; notes by T. Savage (with MCZ 65363–5) indicate that the introduced Bermuda population has retained its arboreal habits.

Though basically insectivorous, I recorded a specimen on Great Bird Island, northeast of Antigua (21.ii.66) eating prickly pear (*Opuntia*) fruit.

Because *A. b. leachi* is restricted to trees (or such substitutes as buildings), land clearing for agriculture has imposed a clumping effect on its otherwise infradispersed population structure.

Distribution. This form occurs throughout the Antigua Bank islands wherever there are trees; it has been introduced into Bermuda.

Relationships. The relationship of this form to *A. b. bimaculatus* is discussed under that form. It was suggested above that the species *bimaculatus* has been derived from an essentially *gingivinus* stock (see *Relationships, A. gingivinus*), and that the species originated on the Antigua Bank. *A. b. leachi* is essentially similar to *A. gingivinus*, except in the following particulars: it averages greener; it grows much larger; it is less notably striped; and (the chief distinction) it has more toe lamellae. All of these may be adaptations to a more arboreal way of life, and marked arboreality seems to be the way in which *leachi* has most effectively niche-segregated from *Anolis wattsi.* If a population of ancestral *Anolis bimaculatus* were isolated from *A. wattsi* sympatry after the initial adaptation away from the *gingivinus* stock had occurred, one might expect to see some, but not all, of these characters present in a species otherwise similar to *gingivinus.* I will argue below that *Anolis nubilus* is just that species.

Etheridge (1964) noted the remarkable jaw sculpturing of adult *A. b. leachi.* All specimens over 100 mm, snout to vent, could match the extreme of sculpture depicted by Etheridge, and one, MCZ 75783, from Long Island, northeast of Antigua, exceeds it. In this specimen, disjunct nodules and balls of bone are set in sockets in the markedly ornate dentary. The adaptive significance of jaw sculpture, or even its genetic basis, is open to speculation.

In summation, *Anolis bimaculatus* is the giant of the *bimaculatus* group (only one other form, a race of *A. marmoratus*—*ferreus* of Marie Galante—exceeds 100 mm). Gigantism seems possible where predation is light, or where the genetic potential to exceed *ca.* 100 mm is well developed and results in predator (kestrel and colubrid snake) immunity. The two races of this species are diverging in important respects (throat fan and nuchal crest size; color) that may result from niche-segregating adaptations to different races of *Anolis wattsi*

Anolis nubilus Garman

Anolis nubilus Garman (1887: 32)

Type. MCZ 6181, W. B. Richardson coll. I have tied the tag to the largest of the three specimens, labeled 6181, and regard it as the type; the other two specimens (fine examples of the species) will be regarded as untagged paratypes.

Type locality. Redonda.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening 2.2 or less times; subdigital lamellae 26–33; male with large, virtually white throat fan; female with bold whitish spots or streak above hind limb insertion.

Squamation. Twenty-five specimens (19 males and 6 females) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; 20–28 (average 24) are contained in the standard distance at midbody. The middorsals average slightly smaller than the midventrals; 22–30 (average 26) are contained in the standard distance; they are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to granules; 32–44 (average 38) are contained in the standard distance six scales lateral to the dorsal midline. The digital dilations are broad and "raised"; there are 26–33 (average 30) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. Both sexes are a very dingy, dark grey-brown and can change to grey-green or grey-blue. The venter is dirty grey. The male throat fan is virtually white (very pale grey), usually with a very faint greenish or yellowish wash, and sometimes with faint blotches of these colors; the scales are white or pale grey. The orbital skin is sometimes slightly yellower than the rest of the head, but not distinctively colored. There are ashy or white flecks on the trunk and legs; these augment the vague longitudinal striping of the female, and are especially prominent over the hind limb insertion. The female has a flank stripe far better delimited than the male.

The color patterns of both sexes are shown on Plate 1.

Size and sexual dimorphism. The largest specimen ever collected, a male, is the type, MCZ 6181: 81 mm, snout to vent. Of the more recently collected material, the largest male is MCZ 82934, taken by me 2 August 1964: 72 mm; this is not as large as one of the paratypes, a 75 mm male. The smallest apparently mature male is 53 mm: MCZ 82940. The largest female is 52 mm: MCZ 82942. The smallest female with eggs is 50 mm: MCZ 82944. With only 25 specimens, only six of them females, I believe the available data on size is incomplete. Only two females are surely mature (those noted above); the species probably grows as large today as it ever did, though the effect of goats on the natural vegetation of Redonda may have so increased vulnerability to bird predation that large specimens are now very rare.

As in *Anolis bimaculatus*, sexual dimorphism is strong in size, weak in coloration, and nonexistent in squamation. In both sexes the standard distance is 17–20 (average 18) per cent of the snout-vent length.

Population structure and ecology. Anolis nubilus is not abundant, but occurs all over Redonda. Owing to the lack of trees, it seems to dwell mostly in the shade of large rocks close to ground. In the ruins of the old building and on the one tree (a *Casuarina*, apparently inedible even to goats), *A. nubilus* climb as high as they can get: about fifteen feet. This species must compete with the large, glossy black ground lizard, *Ameiva atrata*, for at least some of its food. Surely Redonda once supported more vegetation, and presumably *Anolis nubilus* then had an easier life. The feral goats should be extirpated on this remarkable island, whose only known nonflying vertebrates are species found nowhere else on earth. The sex ratio is apparently balanced despite the normal bias for male captures.

Distribution. Anolis nubilus occurs only on Redonda. This tiny islet is exceedingly steep-to, and rises nearly 1000 feet out of the sea. There is virtually no surrounding bank, and the full swell of the western North Atlantic pounds Redonda's cliffs. A tiny, nearly vertical gut on the leeward side provides the only access to the top of the islet up the cliffs; great blocks of basalt lie at the foot of this gut, and one's original entrance to Redonda is made by jumping onto these blocks as the boat goes past them. It is about like jumping from a moving elevator onto a card table, except that elevators give more notice of directional reversals. Getting on Redonda is easy compared to All-a-Wash or Kick-'em-Jenny (in the Grenadines), but getting on is just the beginning.

The islet is a great block of igneous extrusives: strata of basalt and the peculiarly conglomeratelike, porphyritic material so often the result of Antillean vulcanism. The top of Redonda is a rolling wold, and a favorite place of innumerable nesting sea birds; the gut provides a route for their guano to descend the cliffs, and it dries to a thick powder there. Because of its leeward location, a chimney effect is produced in the gut, and the guano dust, mixed with the volcanic sand weathered from the parent rock, tends to rise when disturbed. As one toils up the gut under the tropical sun, one is accompanied by a cloud of this dust, which soon mingles with one's own sweat to produce a wondrously aromatic and abrasive, though rather gluey, bath. At the top, jumbles of rocks and clumps of prickly pear rise gently to the old ruins, complete with a hedge of *Bougainvillea* and the single tree. This is the home of *Anolis nubilus.*

Relationships. Underwood (1959) provisionally synonymized this species with *Anolis lividus*, its closest neighbor to the south, on Montserrat. This has always seemed incomprehensible to me in view of the obvious distinctions between the forms: ear shape and coloration. It was quite surprising to me, therefore, when Dr. Albert

Schwartz (*in litt.*) reported that he, too, regarded *nubilus* and *lividus* as relatives (though not, I hasten to add, as synonyms). Assessments of relationship are always more subjective than we usually like to admit: I usually begin to associate a species when first encountered—whether consciously or subconsciously—with the other species it somehow looks like; this is long before any counts or measurements have been made, of course. To me, *Anolis nubilus* looked and acted like a near relative of *bimaculatus* or *gingivinus*, not like a near relative of *lividus* or its very close ally *marmoratus.* The male throat fan is large, as in the latter species; there is no indication of jaw sculpture, and the ear opening is far more oval than in *bimaculatus* itself (though that is true of *gingivinus* also). However, the manner of expression of sexual dimorphism (size more than color), the high lamellae counts, and the dull hues somewhat vindicate my original view; no more compelling lines of evidence are presently available.

I believe that *Anolis nubilus* was derived from the autochthonous Antigua Bank *bimaculatus* stock at a time not long after the *bimaculatus* stock had begun divergence from its *gingivinus* ancestor, and at about the same time as *bimaculatus* stock also colonized the St. Kitts Bank. Thus, *A. bimaculatus leachi* was evolving, as the original *bimaculatus,* away from *gingivinus* because of sympatry with *wattsi;* when it colonized the St. Kitts Bank, it remained in sympatry (or ecologically zoned parapatry) with an *Anolis wattsi,* and maintained enough of a parallel component in its evolution as a result to remain an *Anolis bimaculatus. Anolis nubilus,* the product of a contemporaneous colonization of Redonda, went out of *wattsi* sympatry, and retained both its basically *gingivinus*-like characters (full sized fan, oval ear, dull hues) and its pro-*bimaculatus* adaptations (high lamellae counts, large size); it has adaptively stagnated in these respects ever since. The faded fan and ashy markings of *Anolius nubilus* are certainly its own innovations.

Anolis lividus Garman

Anolis lividus Garman (1887: 32)

Type. MCZ 6167, S. Garman coll.

Type locality. Montserrat; here restricted to the principal town of Plymouth, where this species is abundant.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth or weakly keeled; width of ear opening, at center of ear, contained in height of ear opening 2.3 or more times; eyelids yellow to red; no dark speckles or vermiculation on sides of neck.

Squamation. One hundred fourteen specimens (64 males, 44 females, and 6 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the level of the naris. The midventrals are usually weakly keeled, but sometimes smooth; there are 21–28 (average 25) in the standard distance at midbody. The middorsals are virtually the same size as the midventrals; there are 20–28 (average 24) in the standard distance; they are rather tubercular and sub- or inimbricate. The scales lateral to the middorsals grade rapidly to dorsal granules: 30–39 (average 35) in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary, and of the "raised" type; there are 20–27 (average 23) subdigital lamellae under the second and third phalanges of the fourth toe.

I previously (Lazell, 1964a: 372) stated that the ventrals of *Anolis lividus* are always keeled, and that the direction of keeling is a diagnostic distinction from *Anolis marmoratus.* My own collections, made subsequently, provide a sufficient quantity of specimens to negate my previous view: the direction of keeling is more variable than I had supposed, and at least the midventrals may occasionally be smooth. (See *Relationships*, below, and *Anolis marmoratus.*)

Coloration. This is a basically green anole with yellow to red eyelids; the males are bright, and shade from brownish green on the head through plain or yellow-green on the trunk to blue-green on the tail. The females are olive-green or brown and have the dullest eyelid colors: yellow to orange; they have striped, ladder, or obsolete middorsal patterns. The ventral surfaces are cream, yellow, or light green.

The male throat fan varies from yellow to olive drab, and has white to green scales.

Both sexes turn darker and browner when upset.

All of the above variation can be seen in the Plymouth population. This species was seen and described alive by Underwood (1959: 199), and further described in detail by Auffenberg and King *in* Williams (1962: 456–460). Only the following points need to be added:

The light (whitish) spotting is an individual variation, not a result of color change; it is quite constant in those specimens that have it, and is enhanced by color change to the dark phase. Females may have light speckles as well as males, but these markings reach their extreme of boldness in the latter.

Specimens from the northwest part of the island average the yellowest: males are frequently bright yellow-green (e. g., MCZ 82032–7, Woodlands).

Specimens from the northeast part of the island average browner than most in Plymouth, and occasionally have dull orange or reddish brown blotches on the nape (e. g., MCZ 82035–7, Farm Estate).

Specimens from remnant rain forest on Mount Chance (e. g., MCZ 82042–3) are at the blue-green extreme of variation.

Adult color patterns are shown on Plate 2.

Size and sexual dimorphism. The largest specimen of this species I have seen is a male, 70 mm, snout to vent (MCZ 82044, Farm Estate); the smallest apparently mature male is 44 mm (MCZ 55701, Plymouth). The largest female examined was 52 mm (MCZ 82051, Farm Estate); the smallest mature female was 40 mm (MCZ 75394, Plymouth). Sexual dimorphism is far more striking in coloration than in size, and does not exist in squamation. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis lividus is ubiquitous and infradispersed throughout Montserrat. Males usually perch from two to eight feet above the ground on a vertical substrate; females and juveniles may be anywhere, but tend to climb less high than males. Both sexes frequently forage on the ground. Generally, the species is extremely abundant, but individuals may be difficult to locate over about 2500 feet on the one high peak: Mount Chance. Field observations indicate a balanced sex ratio.

Distribution. This species is confined to Montserrat, and is found everywhere there.

Relationships. Underwood's (1959) association of this species with *A. nubilus* of Redonda does not fit with my views at all, as discussed under that form.

Anolis lividus and *Anolis marmoratus* are very closely allied. My collections have obliterated the one squamational distinction I thought valid (see *Squamation*, above). The extreme diversity of the twelve subspecies of *A. marmoratus* in morphological characters is a severe handicap in framing species level diagnosis. The eyelid color of *A. lividus* can be matched by the *marmoratus* races *desiradei* and occasionally *chrysops;* both of these forms have dark vermiculation, at least on the neck. *Anolis lividus* seems definitely to possess an evolutionary role uniquely its own, and no useful purpose would be served by allying it subspecifically with *marmoratus.*

Anolis marmoratus Duméril and Bibron

Anolis marmoratus Duméril and Bibron (1837, p. 139)

Type. MNHN Ig. 43. Plee coll.

Type locality. Capesterre, La Guadeloupe.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; ventrals smooth or weakly keeled; width of ear opening, at center of ear, contained in height of ear opening 2.3 or more times; eyelids either not yellow to red, or if so colored, then dark speckles or vermiculation present on the neck.

Remarks. This is the most complex rassenkreis in Lesser Antillean Iguanidae; twelve parapatric or dichopatric forms, distinct in coloration, and frequently in squamation, are found on the three banks of the Guadeloupéen archipelago. I previously (Lazell, 1964a) gave each of these forms detailed consideration and have provided an exhaustive general discourse on the species as a whole; this work should be consulted for information not given below. Presently, I shall repeat this information only through the diagnosis of each form; a comment, including information obtained since 1961 (when the collections for the 1964 report were made), is given for each subspecies; a general map of their ranges is provided (Fig. 5); finally, a discussion of the relationships of the species is given after the subspecies accounts. Here is a species upon which the physiographic and meteorologic peculiarities of the Lesser Antilles have combined to produce ecotypic races developed to a truly dramatic extent (see Introduction).

Population structure and ecology. All of the lowland races of *Anolis marmoratus* are, or were, evenly dispersed, rather than clumped, in population structure. Cultivation has cleared large areas, especially within the ranges of the races *marmoratus, setosus,* and *speciosus,* and this has limited the infradispersion of these forms somewhat. Except for *alliaceus,* which has a distinctive ecology (see below and Lazell, 1964a), all the remaining races occupy relatively dry country; they are abundant wherever bush or trees occur. Both sexes may forage on the ground; females and juveniles usually do. Males tend to perch on any vertical substrate, somewhat higher, on the average, than females: from three to ten feet.

Anolis marmoratus marmoratus Duméril and Bibron

Anolis marmoratus Duméril and Bibron (1837: 139)

Type. MNHP Ig. 43, no date, coll. Plee, *fide* Underwood (1959).

Type locality. Capesterre, La Guadeloupe.

Diagnosis. Dorsal scales in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green, changing to brown, snout suffused with orange; head, neck, and orbital area boldly marbled with bright orange; throat fan light orange-yellow scales. Adult female green, with an obsolete or dully striped middorsal pattern.

Comments. Fresh material from Bois Debut (JDL 282–291) provides a male larger than any other *Anolis marmoratus* ever recorded, except some *A. m. ferreus:* 82 mm, snout to vent (JDL 282). The smallest apparently mature male is 53 mm (MCZ 71219, Carangaise). Mature females range from 54 mm (MCZ 71222, Carangaise) to 48 mm (MCZ 71200, Bananier). There are 21–28 (average 25) middorsals in the standard distance. Adults are shown on Plate 2.

This form is confined to the plain of Capesterre: well-watered lowland to windward of the central, barrier range of La Guadeloupe.

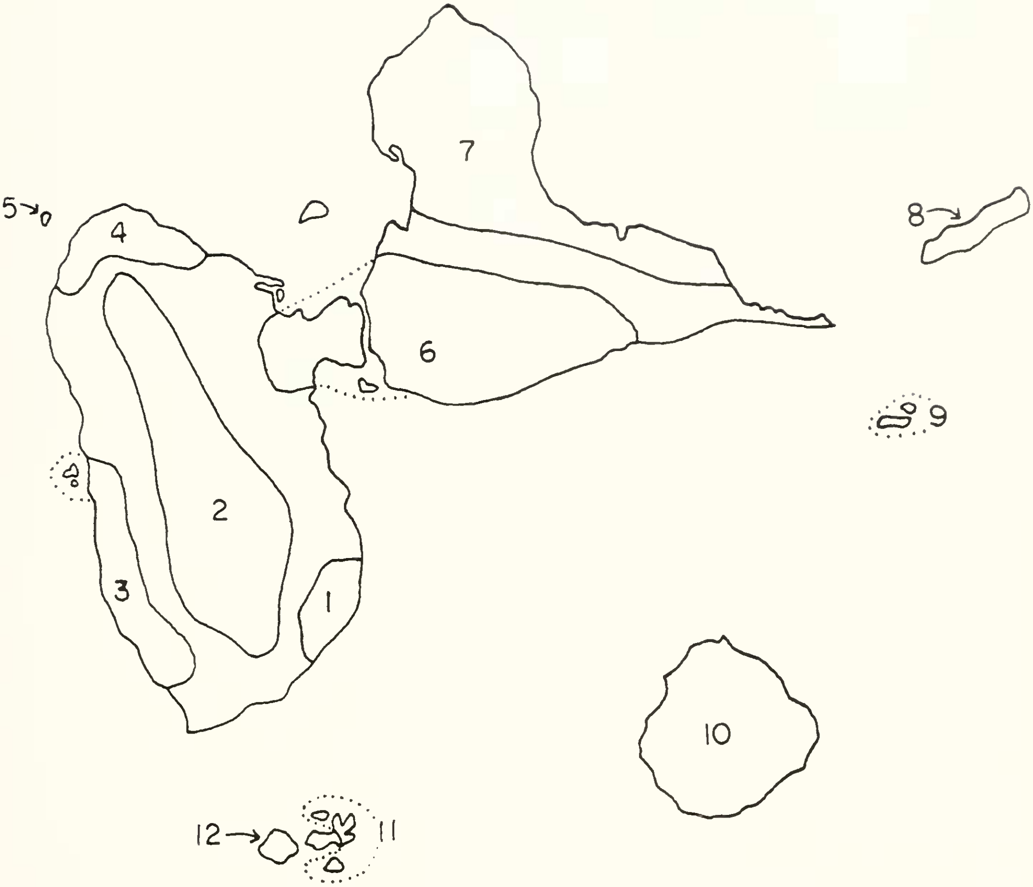

Figure 5. The Guadeloupéen archipelago, showing the ranges of the subspecies of *Anolis marmoratus*: 1. nominate *marmoratus*; 2. *alliaceus*; 3. *girafus*; 4. *setosus*; 5. *kahouannensis*; 6. *speciosus*; 7. *inornatus*; 8. *desiradei*; 9. *chrysops*; 10. *ferreus*; 11. *terraealtae*; 12. *caryae*.

Anolis marmoratus alliaceus Cope

Anolis alliaceus Cope (1864: 175)

Type. BMNH 946.8.28.96, *fide* Underwood (1959).

Type locality. Maison Forestier du Matouba, elevation 700 meters, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green with no blue or bluish pigment in this ground color; palpebral area of orbit white in the light phase, changing to grey as the animal turns dark green; dark dots, tending to run together, scattered over the anterior and dorsal surfaces, and set off by pale cream to yellow borders; throat fan deep orange with green scales. Adult female green with mottled middorsal pattern and small light or dark dots anteriorly.

Comments. Fresh material includes a pair taken at Refuge Joseph Bourgeoise, south slope of Soufrière (JDL 292–3) and a magnificent male taken at Col des Mamelles (JDL 294). The largest male is 74 mm (MCZ 71338, Maison Forestier du Matouba); the smallest mature male is 48 mm (MCZ 71342, Maison Forestier du Matouba). The largest female is 57 mm

(MCZ 71344, Maison Forestier du Matouba); the smallest mature female is 43 mm (north ridge Morne Monstique *ca.* 650 m). There are 24–31 (average 28) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the montane rain forest ecological zone.

Anolis marmoratus girafus Lazell

Anolis marmoratus girafus Lazell (1964a: 377)

Type. MCZ 71259, collected 14 August 1961 by J. D. Lazell.

Type locality. Vieux Habitants, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 25 to 30 (average 28) subdigital lamellae; adult male blue-green to brown, always browner on the head and neck and always at least bluish on the posterior body and tail base; pale streaks and stipples, usually running together to form stripes that produce a reticulate pattern isolating dark spots, on the lateral trunk; throat fan pumpkin yellow with cream-colored to white scales. Adult female pale grey-brown with broken middorsal pattern.

Comments. Fresh material is from Les Ilets de Pigeon, off Malendure: MCZ 81863–7 (Nord), and 81868–72 (Sud). The largest male is the type: 75 mm; the smallest mature male is 56 mm (MCZ 71324, Boulliante), the largest female is 56 mm (MCZ 71286, Baillif); the smallest mature female is 42 mm (MCZ 71337, Malendure). There are 20–30 (average 25) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the arid coast in the rain shadow of the central barrier range of La Guadeloupe.

Anolis marmoratus setosus Lazell

Anolis marmoratus setosus Lazell (1964a: 380)

Type. MCZ 70813, collected 11 August 1961 by J. D. Lazell, Jr.

Type locality. Pointe Allegre, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 22 to 28 (average 25) subdigital lamellae; dorsal scales spinose, those of the nape region so much taller than broad that a distinctly furred effect is produced; adult male blue-green with sooty transverse markings and a dark stripe through eye indicated when changing to the dark phase; throat fan yellow with greenish scales; belly pale, but without yellow tint. Adult female without a middorsal pattern as such, but with a variegation of green, brown, slate, and white speckles and blotches on dorsum, and bold, dark streaks on the lateral venter.

Comments. Females may have striped, ladder, or obsolete middorsal patterns. The largest male is 69 mm (MCZ 70820, Deshaies), not the type as I previously stated (Lazell, 1964a: 381). The smallest mature male is 48 mm (MCZ 70816, Pointe Allegre). The largest female is 51 mm (MCZ 70829, Deshaies); the smallest mature females are both 44 mm (MCZ 10417 and 10425, Ste. Rose). There are 26–34 (average 30) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the mesic coast at the north end of La Guadeloupe, where the barrier range is lowest.

Anolis marmoratus kahouannensis Lazell

Anolis marmoratus kahouannensis Lazell (1964a: 382)

Type. MCZ 70791, collected 28 August 1961 by J. D. Lazell, Jr.

Type locality. Ilet-à-Kahouanne, Guadeloupe Passage, northwest of La Guadeloupe.

Diagnosis. Dorsals in the standard distance 30 to 38 (average 33); 22 to 28 (average 25) subdigital lamellae; dorsal scales conical, producing a bulldog-collar-spike effect on the nape; adult male chartreuse (= bright yellow-green) with no markings except bluish washes on the head and chin;

belly bright yellow; throat fan bright yellow with yellow scales. Adult female chartreuse with a bright yellow belly and no markings except occasional traces of a ladder middorsal pattern.

Comments. Additional specimens are ASFS X6055–7 (two males and a female) collected by Richard Thomas on the Ilet-à-Kahouanne, 4 March 1963. The largest specimen is 73 mm: the type. The smallest mature male is 57 mm (MCZ 70795). The mature females are all either 47 mm (MCZ 70799) or 48 mm (the rest); a 43 mm female (ASFS X6057) does not contain eggs. There are 23–31 (average 27) middorsals in the standard distance. Adults are shown on Plate 2.

This form presumably owes its distinctiveness to isolation, rather than ecological zonation.

Anolis marmoratus speciosus Garman

Anolis speciosus Garman (1887: 45)

Type. MCZ 6172, collected by Richardson, March, 1886.

Type locality. Pointe-à-Pitre, Grande Terre.

Diagnosis. Dorsals in the standard distance 32 to 50 (average 40); 20 to 26 (average 23) subdigital lamellae; adult male green, without dorsal markings; venter brightly washed with yellow; orbital area sky blue; throat fan sulfur yellow with greenish scales. Adult female olive with ladder or striped middorsal pattern.

Comments. Additional specimens are MCZ 80533–4, "Guadeloupe," George Gorman coll., and MCZ 81883–91, Ste. Anne, Grande Terre, taken by me 13.viii.64. The largest specimen, a male, is 73 mm, snout to vent (MCZ 70978, Ilet-à-Cochons), not MCZ 70961, as previously stated (Lazell, 1964a: 385). The smallest apparently mature male is 48 mm (MCZ 70974, Abymes). The largest female is 52 mm (MCZ 70957, Baie Mahault); the smallest mature females are both 43 mm (MCZ 70945, Ste. Anne, and 70960, Baie Mahault). There are 26–35 (average 31) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the main body of well-watered lowland to windward of the central barrier range of La Guadeloupe.

Anolis marmoratus inornatus Lazell

Anolis marmoratus inornatus Lazell (1954a: 386)

Type. MCZ 71036, collected 13 August 1961 by J. D. Lazell.

Type locality. Anse Bertrand, Grande Terre.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 25) subdigital lamellae; adult male pale grey-green on trunk, rich brown on head; orbital area brown; belly pale lime-green; throat fan yellow with white to cream-colored scales; flank stripe indicated. Adult female pale grey-brown with striped middorsal pattern and flank stripe.

Comments. Females may have ladder middorsal patterns. Additional specimens are MCZ 81846–52, collected by me at Moule, Grande Terre, 9.viii.64. The largest specimen examined, a male, is 65 mm, snout to vent (MCZ 71049, town of Ste. Marguerite); my previous record of 75 mm, given for the type (Lazell, 1964a: 386) is in error, and resulted from a reversal of the digits in 57 mm, the correct measurement for the specimen. The smallest apparently mature male examined is 45 mm (MCZ 71025). The largest females are both 50 mm (MCZ 71018 and 81851, Moule); the smallest mature female is 40 mm (MCZ 71057, town of Ste. Marguerite). There are 26–36 (average 31) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is dry; it is too far to windward of La Guadeloupe to be climatically affected.

Anolis marmoratus desiradei Lazell

Anolis marmoratus desiradei Lazell (1964a: 387)

Type. MCZ 71068, collected 14 September 1961 by J. D. Lazell, Jr.

Type locality. Grande Anse, La Désirade.

Diagnosis. Dorsals in the standard distance 32 to 50 (average 40); 22 to 28 (average 25) subdigital lamellae; adult male pale greenish with yellow wash on sides and yellow belly; dorsal surfaces extensively vermiculated with darker grey-brown; throat fan yellow with white to cream-colored scales; orbital area bright rust red; chin yellow with bold blue-grey streaking. Adult female grey-greenish with grey head and yellow belly; middorsal pattern obsolete or dully striped.

Comments. Previously (Lazell, 1964a: 388) I stated of females: "there is no indication of vermiculation." That is untrue, and results from failing to note the vermiculation of living females in my field notes, and then assuming that the preserved specimens (whose patterns I did not examine closely) were unmarked in life. Fresh material collected by me (MCZ 81872–82, Grande Anse) documents female vermiculation. The largest specimen measured, the type, was 80 mm, snout to vent, fresh dead. The smallest apparently mature male is 51 mm (MCZ 62211, Ravine La Rivière). The three largest females are 53 mm (MCZ 71107–8, and 71111, Pointe Double); the smallest mature female is 44 mm (MCZ 71098, Le Souffleur). There are 21–31 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus chrysops Lazell

Anolis marmoratus chrysops Lazell (1964a: 389)

Type. MCZ 70649, collected 4 September 1961, by J. D. Lazell, Jr.

Type locality. Terre de Haut, Les Iles de la Petite Terre.

Diagnosis. Dorsals in the standard distance 30 to 42 (average 36); 22 to 28 (average 25) subdigital lamellae; adult male somber green-grey with bright yellow suffusion on the sides and bright yellow belly; vermiculations present on the anterior trunk and nape, at least, and dark dotting usually present on remaining dorsal surfaces; orbital area red-gold; chin entirely blue-grey; throat fan yellow with pale yellow scales. Adult female grey with yellow belly, an obscure striped middorsal pattern, and a brief flank stripe.

Comments. All three topotypic females (originally MCZ 70663–5) are missing in 1967; presumably they were traded or given away as a matter of curatorial routine, without consideration of the effect of this action on the type series. The largest male, the type, was 73 mm, snout to vent, fresh dead. The smallest apparently mature male is 62 mm (MCZ 70662, Terre de Haut). The largest females are both 48 mm (MCZ 70653 and 70655, Trou Canard, Terre de Bas); the only other remaining female is mature and measures 46 mm (MCZ 70654, also from Trou Canard, Terre de Bas). There are 23–30 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus ferreus (Cope)

Xiphosurus ferreus Cope (1864: 168)
Anolis asper Garman (1887: 31)

Type. BMNH 1946.8.5.59, no collector, no date.

Type locality. Morne Constant, Marie Galante.

Diagnosis. Dorsals in the standard distance 22 to 33 (average 28); 25 to 30 (average 28) subdigital lamellae; adult male somber grey-brown becoming greener posteriorly; dorsum sprinkled with dark spots seldom coalescing to form short vermiculations; suffusions, often forming blotches, of yellow laterally; orbital area dull yellow; uniform blue-grey of chin often invading otherwise yellow throat fan with yellow scales. Adult female grey-brown to greenish with brief flank stripe, obsolete middorsal pattern, and a very pale yellowish belly.

Comments. The largest male examined was 119 mm, snout to vent, fresh dead (MCZ 70767, Vieux Fort); the smallest apparently mature male is 63 mm (MCZ

70769, Vieux Fort). The largest female is 65 mm (MCZ 70763, Grand Bourg); the smallest mature female is 50 mm (MCZ 70780, Courbaril). There are 19–26 (average 22) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus terraealtae Barbour

Anolis terraealtae Barbour (1915: 76)

Type. MCZ 10627, collected by Noble, no date.

Type locality. Pompière, Terre de Haut, Les Iles des Saintes.

Diagnosis. Dorsals in the standard distance 28 to 40 (average 33); 20 to 26 (average 25) subdigital lamellae; adult male grey-brown to green-brown, without dark speckles or vermiculations; large blotches of bright yellow laterally and on nape fading to suffusions on posterior body and belly; yellow of orbital area often confluent with yellow blotching of nape and trunk; throat fan yellow with yellow scales. Adult female grey-brown with a faint flank stripe briefly indicated and a striped or ladder middorsal pattern.

Comments. The largest specimen was 80 mm, snout to vent (MCZ 70687, Pointe Basse, Grande Ilet), fresh dead. The smallest apparently mature male is 54 mm (MCZ 70713, Pompière, Terre de Haut). The largest females are 54 mm (MCZ 70714–5, Pompière, and 70693–4, Pointe Basse, Grande Ilet); the two smallest mature females are 51 mm (MCZ 70695, Pointe Basse, Grande Ilet, and 70756, Ilet-a-Cabrit). There are 22–30 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is, like that of *desiradei*, *chrysops*, and *ferreus*, the arid lowland typical of those islands too low in elevation to stop significant rainfall. See the following form, however.

The type locality, on eastern Terre de Haut, is called "Pont Pierre" on some maps; this seems odd, as there is no bridge or likely place to put a bridge.

I could not find the type specimen, MCZ 10627, for my 1964 account, but expected it to turn up eventually as I examined the rest of the Lesser Antillean anoles; it has not. Underwood (1959) lists it as a specimen examined, but this means little, as he seems to have recorded specimens from bottle labels, and thus listed many specimens as "examined" that have not been in the collection for decades. Since the paratypes are present and serve to identify the form on scale characters, I see no present need to designate a neotype.

Anolis marmoratus caryae Lazell

Anolis marmoratus caryae Lazell (1964a: 394)

Type. MCZ 70666, collected 6 September 1961 by J. D. Lazell, Jr.

Type locality. The town of Terre de Bas, Terre de Bas, Les Iles des Saintes.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 23) subdigital lamellae; adult male pale green, becoming bright green posteriorly; a faint wash of yellow on abdomen, rest of belly lime green; fine vermiculations coalesce on the back of the head and the nape to produce a grey appearance; posteriorly these fine vermiculations produce distinct pale grey transverse markings; a pale, whitish flank stripe accentuated in the costal region by a lack of vermiculation; throat fan bright yellow with yellow scales; orbital area cream-colored. Adult female pale grey-green with ladder middorsal pattern and striking flank stripe set off by dark speckles above and below.

Comments. Additional, fresh material was taken by me at the type locality (MCZ 81853–62) and on the northwest side of Pointe Sud (MCZ 81836–45) on 10–11.viii.64. One of the new males (MCZ 81854) measures 75 mm, snout to vent, after more than two years in preservative; this specimen was no doubt larger than the type (75 mm, fresh dead) when alive. The smallest apparently mature male is 56 mm (MCZ 81857, town of Terre de Bas). The largest female is 55 mm (MCZ 70682, town of Terre de Bas); the smallest mature female is 46 mm (MCZ 81845, northwest side, Pointe Sud). Females may have simply striped middorsal patterns. There are 27–34 (average 30) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is a low snag island: Terre de Bas. It does impede sufficient cumulus to have a distinctly wetter climate than do the islands to the east of it.

Relationships. Although striking sexual dimorphism in color is apparent in nominate *marmoratus, alliaceus,* and *speciosus,* it is less notable in the other subspecies. Sexual dimorphism in size is better developed in this species, as a whole, than in *A. lividus,* less well developed than in *A. bimaculatus.* There is no significant dimorphism in squamation. Geological evidence, discussed under Evolution below, indicates that differentiation of some of the subspecies, like *kahouannensis, desiradei,* and *chrysops,* has probably been post-Wisconsin. Behavioral evidence with captives indicates that forms strongly distinct in coloration, like *marmoratus* and *speciosus,* would not interbreed directly; females of *marmoratus* that readily accept males of their subspecies in captivity do not respond to *speciosus* males. In the field there is a large zone of intergradation between these forms; they are presumably subspecies that have evolved as a single land area was colonized, not the result of separate colonizing populations that evolved independently until they covered enough geographic area to meet. The selection pressures for their distinctive color patterns must be strong, or the distinctions would never have arisen; in the zone of intergradation, selection pressures must cline with the characters: intermediate anoles do best in an intermediate habitat. Thus, it is not surprising that a zone of intergradation exists between two forms that, if abruptly transported into sympatry, may not interbreed.

If we suppose that the sum of genetic distinctions between *A. lividus* and *A. m. marmoratus* are no greater than between *A. m. marmoratus* and *A. m. speciosus* (an assumption surely faulty owing to the magnitude of the actual isolation of the two former), could we assume that *lividus* and *marmoratus* would introgress if transported into sympatry? Quite the contrary, the evidence is that these anoles are so color sensitive that they would not. The only *marmoratus* forms that have the eyelid color of *A. lividus, desiradei* and *chrysops,* are so different in general body coloration that a similar interpretation is in order.

Gorman and Atkins (1968b) found *A. m. marmoratus* and the very divergent subspecies *A. m. ferreus* to be karyotypically similar to each other, and to other Lesser Antillean members of the *bimaculatus* group, except *A. acutus* (see *Relationships* of that species) and *A. oculatus* of Dominica. It is not, therefore, possible to make much of a case for close relationship between the species *marmoratus* and *oculatus,* despite their geographic proximity.

Anolis oculatus (Cope)

Xiphosurus oculatus Cope (1879: 274)

Lectotype. USNM 10145, by present designation.

Type locality. Roseau, Dominica (see Lazell, 1962: 468).

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) in which the prenasal is subrectangular, and fails to extend posteriorly to the anterior level of the naris.

Remarks. Anolis oculatus is the most bizarre member of the *bimaculatus* group, and one of the most peculiar members of its huge and diverse genus. It is remarkable and distinct in ways that I could not have known about when I wrote the original report on the species (Lazell, 1962); also, it is remarkable and distinct in ways which I simply did not notice at the time of that report. My previous work on *A. oculatus,* while correct in major taxo-

PLATE 2

9\. *Anolis bimaculatus bimaculatus*: male, MCZ 75469; female, MCZ 75473; Basseterre, St. Kitts.

10\. *Anolis bimaculatus leachi*: male, MCZ 82108; female, MCZ 82109; Ten Pound Bay, Green Island, E of Antigua.

11\. *Anolis lividus*: uniform male, MCZ 82044, Farm Estate; female, MCZ 82051, Farm Estate; spotted male, MCZ 82043; S summit, Mt. Chance, Montserrat.

12\. *Anolis marmoratus marmoratus*: male, JDL 282; female, JDL 288; Bois Debut, La Guadeloupe.

13\. *Anolis marmoratus alliaceus*: male, MCZ 71358; female, MCZ 71359; N ridge, Morne Moustique, ca. 650 m, La Guadeloupe.

14\. *Anolis marmoratus kahouannensis*: male, MCZ 70791; female, MCZ 70796; Ilet-à-Kahouanne, NW of La Guadeloupe.

15\. *Anolis marmoratus speciosus*: male, MCZ 70925; female, MCZ 70932; Gosier, Grande Terre.

16\. *Anolis marmoratus girafus*: male, MCZ 71262; female, MCZ 71268; Vieux Habitants, La Guadeloupe.

17\. *Anolis marmoratus setosus*: male, MCZ 70813; female, MCZ 70816; Pointe Allegre, La Guadeloupe.

18\. *Anolis marmoratus inornatus*: male, MCZ 71036, Anse Bertrand; female, MCZ 71054; town of Ste. Marguerite, Grande Terre.

19\. *Anolis marmoratus desiradei*: male, MCZ 71068; female, MCZ 71076; Grande Anse, La Desirade.

20\. *Anolis marmoratus chrysops*: male, MCZ 70649, Terre de Haut; female, MCZ 70653; Trou Canard, Terre de Bas, Les Iles de la Petite Terre.

21\. *Anolis marmoratus ferreus*: male, MCZ 70748; female, MCZ 70757; Morne Constant, Marie Galante.

22\. *Anolis marmoratus terraealtae*: male, MCZ 70687; female, MCZ 70694; Pointe Basse, Grande Ilet, Les Iles des Saintes.

23\. *Anolis marmoratus caryae*: male, MCZ 70666; female, 70672; Terre de Bas, Terre de Bas, Les Iles des Saintes.

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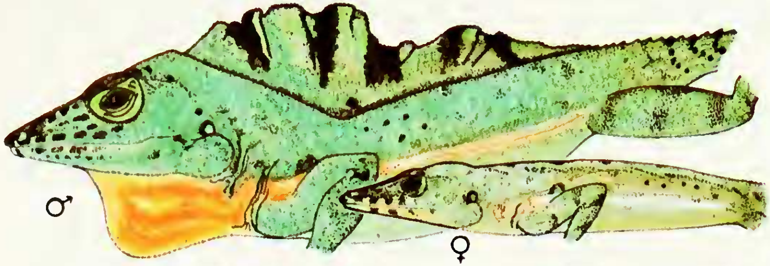

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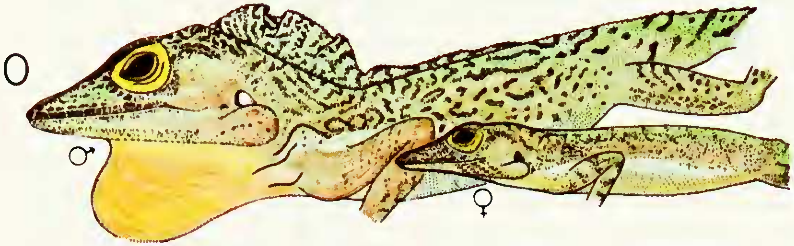

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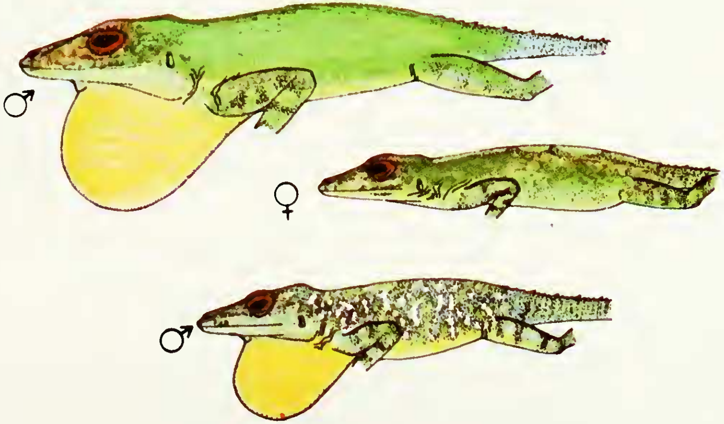

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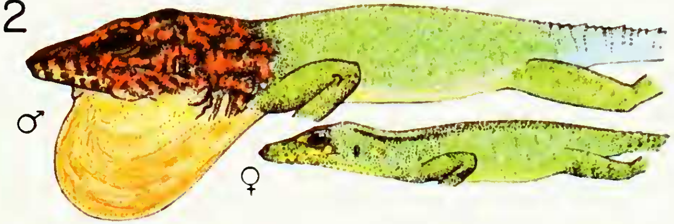

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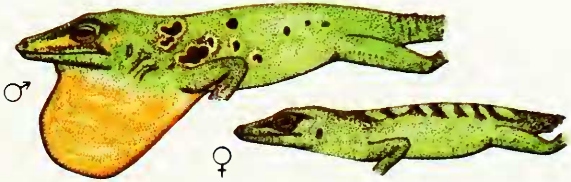

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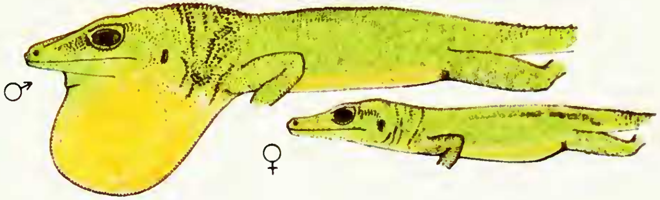

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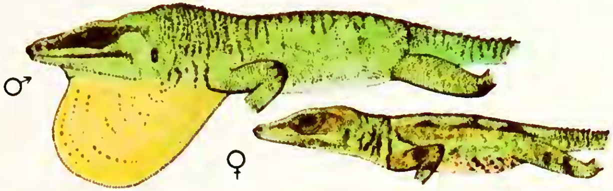

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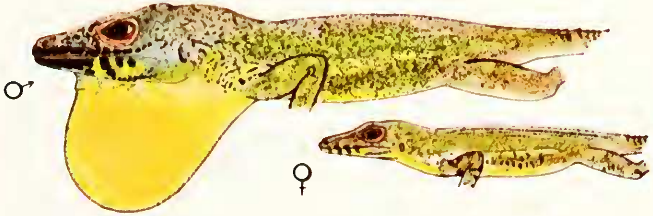

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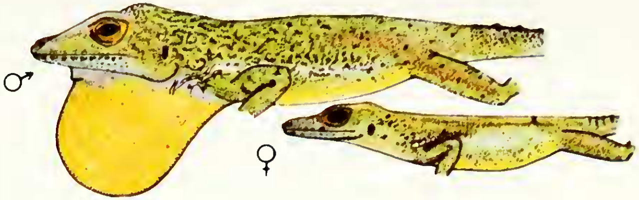

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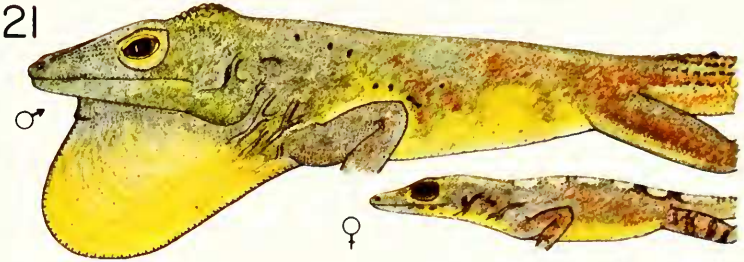

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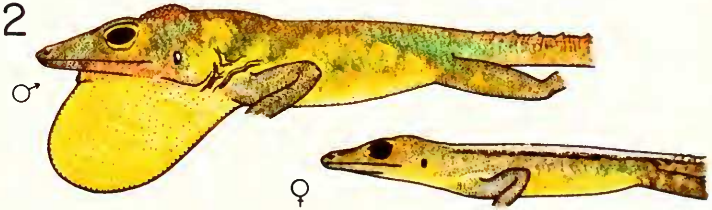

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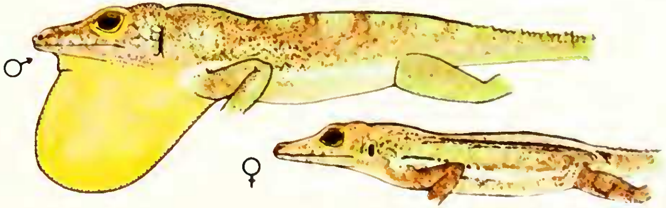

nomic features, was thoroughly unsophisticated. The paper was based largely on field observations, and I paid scant heed to the specimens once they were catalogued into the MCZ. Thus, I missed numerous specimens considerably in excess of what I stated to be the maximum sizes of three of the subspecies, and failed to note scale characters that not only separate *oculatus* from its relatives at the species level, but also aid in the recognition of the four subspecies.

Although I knew the adverse effect of formaldehyde on *Anolis*, I did not know of any "safe" alternative. My specimens were injected with strong formalin and unceremoniously dumped into a gallon jar of "cask rhum." This method of preservation certainly worked, but left a great deal to be desired in quality of material from the standpoint of color retention. After 24 hours in this witches' brew, the specimens were removed, wrapped in rhum-soaked newspaper, and packed in bisquit tins. I kept no field catalogs; the color notes and field data were written on bits of paper, in pencil, and packed with the specimens. The filled tins were shipped back by surface freight. Fortunately, I beat them to Cambridge, and was thus on hand to do the unpacking; otherwise much might have been lost.

In those days, the only air transport to Dominica was a single Grumman Goose that landed twice a week in the open roadstead at Roseau. The only real road on the island was the Trans-Insular, or Imperial, Road. It wound northeastward out of Roseau into the forest. It crossed the spine of volcanic peaks and descended to the windward coast. It wandered, a tiny ribbon of blacktop, through richly cultivated lands nearly to the northern end of Dominica, then turned west, crossed the low col between Morne Diablotin and Morne au Diable, called the Dos d'Ane, to Portsmouth. With good luck, one could make it from Roseau to Portsmouth in about six hours: an airline distance of about fifteen miles. With ill luck, one could not make it at all: far up in the mist of the cloud forest was an infamous slope called simply "The Slips." Many times I have been turned back there.

Another, much shorter, road went south out of Roseau along the leeward coast, then cut inland between Morne Anglais and Morne Plat Pays, descending to the little windward coast town of Grand Bay. As an alternative to the Imperial Road, for the short stretch between Canefield Estate and Pont Cassé, was the then brand new Layou Valley Road. Other than those roads, there were a few, disappointingly short, jeep tracks. In fact, most of my collecting sites were visited on foot or on horseback. It took me ten days on a horse to collect the windward coast of Dominica between Hatten Garden, where the Imperial Road descends, and Grand Bay. One can now drive to Castle Bruce, Rosalie, or even La Plaine —collecting sites along my route in 1959— in an hour or so from Roseau. A good road extends up the leeward east now as far as Colihaut, and will shortly connect to Pointe Ronde and Portsmouth. It is said that "The Slips" no longer slip, but shortly it will no longer matter if they do.

I returned to Dominica in February 1966, to collect fresh alcoholics of the four subspecies. New roads have made important new collecting sites accessible for three of the forms, and new maps have made possible far more precise definition of their ranges. If Dominica and I have changed, at least *Anolis oculatus* remains the same. What is presented below both supplements and emends my original descriptions.

My previous account of this species (Lazell, 1962) provides considerable detail that will not be repeated here. The diagnoses given there, however, applied only to males, and were not as tight as they could be. I have recast them below, and a general map of the four subspecies is here provided: Figure 6.

I did not discuss squamation characters in 1962; these are noted below. A discus-

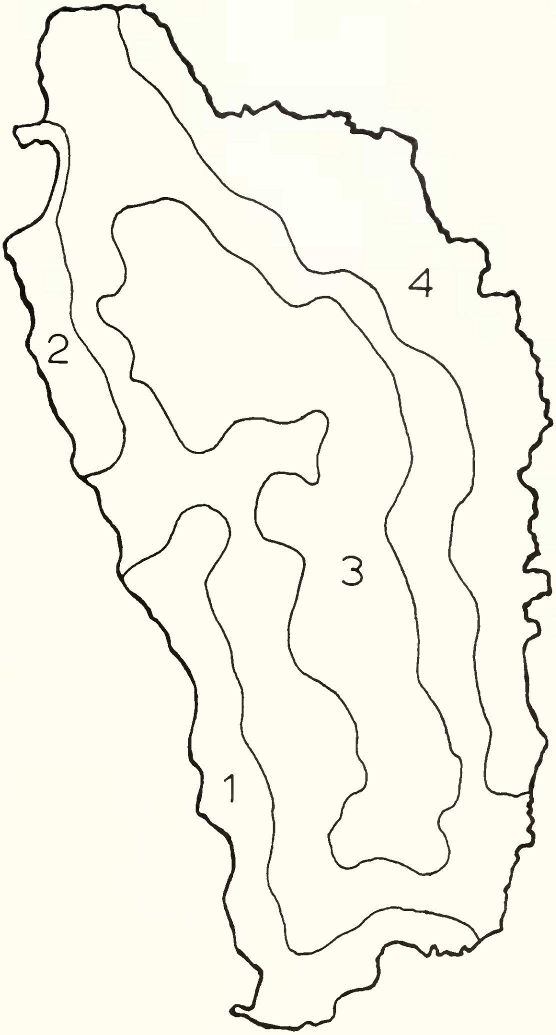

Figure 6. Dominica, showing the ranges of the subspecies of *Anolis oculatus*: 1. nominate *oculatus*; 2. *cabritensis*; 3. *montanus*; 4. *winstoni*.

sion of the relationships of the species is provided after the subspecies accounts. The races of *Anolis oculatus* conform to ecological zonation (see Introduction).

Anolis oculatus oculatus (Cope)

Xiphosurus oculatus Cope (1879: 274)

Type. USNM 10145 (see above).

Type locality. Roseau, Dominica.

Diagnosis. An *Anolis oculatus* with olive to grey-brown ground color; primary spots small, or vague, or absent; little if any black pigment surrounding primary spots of males; secondary spots vague or absent; venter pale yellow to white; male throat fan bright yellow with whitish scales; females with striped middorsal pattern.

Comments. Fresh material is from Goodwill, above Roseau (JDL 245–9) and Fond St. Jean, east of Grand Bay (JDL 273–7);

the latter a range extension. Mature males range from 79 mm, snout to vent (MCZ 60355, Hillsborough) to 44 mm (MCZ 60439, Second Layou River bridge, and JDL 273, Fond St. Jean). Adult females range from 58 mm (MCZ 60369, Roseau) to 42 mm (JDL 276, Fond St. Jean).

There are 20–27 (average 23) midventrals in the standard distance at midbody. There are 20–26 (average 23) middorsals in the standard distance in males, 21–31 (average 26) middorsals in the standard distance in females. There are 35–47 (average 41) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 18–24 (average 21) subdigital lamellae under the second and third phalanges of the fourth toe. The standard distance six scales lateral to the per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3.

This is the form of the mesic southern end of Dominica, where the barrier range is at least at its lowest.

Anolis oculatus cabritensis Lazell

Anolis oculatus cabritensis Lazell (1962: 469)

Type. 60245, Lazell coll., 8.vi.59.

Type locality. The Cabrits (Prince Rupert Point), Dominica.

Diagnosis. An *Anolis oculatus* with grey or pale tan ground color, often overlaid with mustard yellow; primary spots large and bold, set off with ample black pigment in males; secondary spots run together to form irregular stripes or marbling; venter bright yellow to peach; male throat fan bright yellow with whitish scales; females similar but striped.

Comments. Fresh material fills in the range at Anse Gabriel, south of Colihaut (JDL 250–9). Adult males range from 81 mm, snout to vent (MCZ 60258, Pointe Ronde), to 55 mm (MCZ 60314, Picard). Adult females range from 59 mm (MCZ 60275, Pointe Ronde) to 48 mm (MCZ 60274, Pointe Ronde). There are 22–33 (average 28) midventrals in the standard distance at midbody. There are 22–30 (average 26) middorsals in standard distance in both sexes. There are 40–51 (average 45) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 18–24 (average 21) subdigital lamellae under the second and third phalanges of the fourth toe. The standard distance is 16–20 (average 18) per cent of the snout vent length in both sexes.

Adults are shown on Plate 3. This is the form of the arid coast to leeward of the great, central barrier range of Dominica.

Anolis oculatus montanus Lazell

Type. MCZ 60319, Lazell coll., 6.vii.59.

Type locality. Fresh Water Lake, Dominica.

Diagnosis. An *Anolis oculatus* with a green to nearly black ground color; both primary and secondary spots small and bright, black pigment surrounding several anterior spots in males; venter green, often metallic or coppery posteriorly; male throat fan very dark, dull ochre to orange with green or grey-green scales; females similar, usually striped.

Comments. Fresh material is from William Estate (Crete Palmiste), (JDL 206–6) and Brantridge (JDL 306), both in the middle of the range, and from Morne Anglais (JDL 316–323) at its southern terminus; I am once again indebted to Charles A. Winston, and his family, for this latter, excellent series, taken above his home at New Florida on the southwest slope of the mountain.

The largest male is 96 mm, snout to vent (MCZ 60344), from Fond Hunt; the smallest apparently mature male is 49 mm (JDL 321), from Morne Anglais. Mature females range from 64 mm (MCZ 60329, Fresh Water Lake) to 44 mm (MCZ 65930, Fresh Water Lake).

There are 21–27 (average 23), midventrals in the standard distance at midbody.

There are 18–24 (average 21) middorsals in the standard distance in both sexes. There are 32–40 (average 36) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 19–27 (average 22) subdigital lamellae in males, and 18–23 (average 20) in females, under the second and third phalanges of the fourth toe. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3. This is the form of the montane rain forest ecological zone.

Anolis oculatus winstoni Lazell

Anolis oculatus winstoni Lazell (1962: 472)

Type. MCZ 60467, Lazell coll., 29.vi.59.

Type locality. Woodford Hill, Dominica.

Diagnosis. An *Anolis oculatus* with a rich brown ground color; spots small, bright, little differentiated into primary and secondary rows, not surrounded by black pigment; venter peach to bright yellow; male throat fan deep pumpkin yellow with lighter yellow scales; females similar, but usually striped.

Comments. Fresh material is from the type locality, Woodford Hill (JDL 267–71). The largest male is 86 mm (MCZ 60525), from Castle Bruce; the smallest male is 56 mm (MCZ 60486, Woodford Hill). Mature females range from 64 mm (MCZ 80531), from Marigot, to 50 mm (MCZ 60624), from La Plaine.

There are 23–32 (average 28) midventrals in the standard distance at midbody. There are 22–30 (average 27) middorsals in the standard distance in both sexes. There are 37–48 (average 43) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. There are 19–24 (average 22) subdigital lamellae in males, and 18–21 (average 20) in females, under the second and third phalanges of the fourth toe. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3. This is the form of the well-watered lowland to windward of the great, central, barrier range of Dominica.

Relationships. Gorman and Atkins (1968b) have shown *Anolis oculatus* to be karyotypically extreme among *bimaculatus* group anoles: it possesses two pairs of acrocentric macrochromosomes; no acrocentric autosomes are known in any other alpha *Anolis.* The prenasal scale is unique. Also, most males of this species show enlargement of the light scales in some of the spots, frequently to a remarkable (and pathological looking) extent; I have seen only a remote suggestion of this in some *Anolis marmoratus* (e. g., MCZ 81863, a male *A. m. girafus* from Ilet de Pigeon du Nord). *Anolis oculatus* is a rather large species with peculiarly low lamellae counts. Sexual dimorphism is variably expressed in size, color, and squamation, but is not striking in any of these respects.

It would seem that *Anolis oculatus* has long evolved in isolation, and lacks genuinely close relatives.

Anolis luciae Garman

Anolis luciae Garman (1887: 44)
Anolis trinitatis procuratoris Underwood (1959: 214)

Type. MCZ 6175 (not 6173, a series of 19 paratypes, as cited by Underwood, 1959: 213). S. Garman coll., 1887.

Type locality. St. Lucia; here restricted to the principal town and port, Castries.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials extend posteriorly as a series of scales notably larger than those surrounding them to or beyond the level of the posterior edge of the orbit.

Squamation. Two hundred fifty-three specimens of this species (175 males, 70 females, and 8 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: There are 20–29 (average 25) midventrals in the standard distance at midbody; they are smooth, and the same size as the middorsals. There are 20–30 (average 25) middorsals in the standard distance. The dorsal granules decrease rather abruptly in size laterally; there are 33–42 (average 38) in the standard distance six scales lateral to the dorsal midline. The digital dilations are of undistinguished width and of the raised condition; there are 23–31 (average 27) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. Anolis luciae is not a colorful species, though there is some geographic variation in hues. Males from Castries (MCZ 71685–9) are brown to olive with a tannish white belly and chin. The throat fan is very dingy: a greyish yellow or dull orange with white scales; it is frequently brighter posteriorly. The eyelids are pale greenish or tan to white. Color change is to pale apple green with blue tones laterally and on the extremities. The flank stripe is very vague and there is no dorsal pattern. Females (e. g., MCZ 71690) are similar, even duller and browner, show less color change, and have dark chevrons with whitish posterior borders to the tail base.

Specimens from Savanne Edmund (MCZ 71696–708), one of the type localities of "*procuratoris*" Underwood (1959), average darker; frequently the blue tones are extensive and deep, including a blue flank stripe and blue eyelids. Sometimes the bellies have a yellow wash. Throat fans vary from virtually plain grey with a faint greenish wash to brick red with green scales. Females frequently have a dark middorsal stripe in addition to the chevronate markings.

Specimens from the Barre de l'Isle (MCZ 71691–6), Marquis (MCZ 71769–75), between Londonderry and Gertrine (MCZ 71804–9: 13° 47′ N, 61° 00′ 30″ W, the other type locality of "*procuratoris*" Underwood), Dennery (MCZ 71810–7), Micoud (MCZ 71796–803), and Soufrière (MCZ 71786–95), span these extremes. Those from the Barre de l'Isle, Dennery, Micoud, Vieux Fort (MCZ 71737–43), and Moule-à-Chique Lighthouse (MCZ 71744–52) show better flank stripe definition and frequently the males show some dorsal chevronate pattern. Those from other parts of the range agree with Castries specimens. The overall pattern is thus of darker specimens in the interior highlands, paler specimens in coastal regions, and the most patterned specimens from the east and south. All of this variation is modal and clinal; no subspecies can be recognized.

I examined 54 specimens from the southernmost Maria Island (37 males, 10 females, and 7 juveniles), of which 10 (6 males and 4 females: MCZ 71776–85) were collected by me. Although many larger specimens in this population show a peculiar reticulate mottling of dark brown (this is vaguely visible, even in life, on these dark individuals), I cannot find characters that will separate it from the sum of the mainland variation.

The iris of most species of *Anolis* (all in the Lesser Antilles) varies from blackish brown to blue; the complete range, even to turquoise, may be seen in *A. luciae* from Castries, or anywhere else on St. Lucia.

Color patterns of adults are shown on Plate 3.

Size and sexual dimorphism. The largest specimen examined, an adult male, is 91 mm, snout to vent (MCZ 71697, Savanne Edmund); the smallest apparently mature male is 50 mm (MCZ 80450, Castries). The largest female is 63 mm (MCZ 71773, Marquis); the smallest mature female is 48 mm (MCZ 71817, Dennery).

The duller colors of females, and their patterning of chevrons, and frequently a middorsal stripe, are the principal sexual dimorphism; there is no indication of dimorphism in scales. The standard distance is 16 or 17 per cent of the snout-vent length in all specimens examined.

Population structure and ecology. Anolis luciae occupies most of its range alone; *A.*

extremus, from Barbados, and *A. wattsi*, from Antigua, have been introduced into Castries, and at least the former seems to be spreading. Nevertheless, *A. luciae* is not as abundant in most areas as might be expected of a species of ubiquitous habits without competition. Only on the southernmost Maria Island is this species really abundant, by ordinary Lesser Antillean standards. Males perch from three to twelve feet; females and juveniles tend to perch lower. Both sexes forage in bushes, trees, and on the ground; the species is thoroughly infradispersed throughout its range.

Field observations indicate a balanced sex ratio.

One might expect the small rupicolous *A. w. wattsi* to do well on St. Lucia in sympatry with *A. luciae;* it does not, however, seem to spread from the original collection site: the Botanical Garden in Castries. *Anolis extremus,* however, is abundant in Castries and its suburbs. I was convinced that it had spread from its 1962 range when I visited St. Lucia again in 1964. *A. luciae,* strangely, seems no less common within the *A. extremus* area, despite the apparent niche overlap.

Distribution. *Anolis luciae* occurs throughout St. Lucia and on its coastal cays that support more than herb-stage vegetation, like Pigeon (MCZ 71709–19) and the southernmost of the Maria Islands.

Relationships. Gorman and his colleagues have examined relationships of the *Anolis* of the *roquet* group in detail from the viewpoints of blood proteins (Gorman and Dessauer, 1965, 1966), karyotypes (Gorman and Atkins, 1967), and display behavior (Gorman, 1968). The summary work is Gorman and Atkins (1968b). My own morphological examinations confirm Gorman's views, and make possible definite assertions where he presented alternatives; I shall defer all but succinct remarks on the relationships of the species (see Evolution, below).

There is complete agreement: *Anolis luciae* is the closest living form to the ancestral stock of the entire group.

At some time prior to the acquisition of the enlarged sublabial scale row in *luciae*, there must have been two southward invasions of the primitive stock: the first gave rise to *A. griseus* and its derivative *richardi;* the second to *A. trinitatis* and its derivatives *aeneus, extremus,* and *roquet.* At least one extralimital colonization of the *luciae* stock, at a time subsequent to the initial development of the sublabials, gave rise to *A. bonairensis* far to the west. Thus, none of the other Lesser Antillean members of the group possess enlarged posterior sublabials, and *A. bonairensis* does only to an incomplete extent.

Anolis griseus Garman

Anolis griseus Garman (1887: 36)

Lectotype. MCZ 6164, S. Garman coll., 1887. I have tied tag 6164 to the finest adult male, a 117 mm specimen; the remaining five specimens should be recatalogued.

Type locality. St. Vincent; here restricted to the principal town and port, Kingstown (Garman's actual data read "Kingston"; a common error).

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined; sublabial scale row breaks up into undistinguished scales below eye; usually four or fewer scales of the supraorbital semicircles abut on top of head; if more, then interparietal separated from supraorbital semicircles; 11 or fewer (8–11) middorsals contained in ten per cent of the snout-vent length at midbody.

Squamation. Seventy specimens of this species (28 males and 42 females) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: There are 19–30 (average 25) midventrals in the standard distance at midbody; these are smooth, swollen, or tectiform, and much smaller than the middorsals. There are 15–18 (average 16) middorsals in the standard distance. The dorsals decrease abruptly in size laterally; there are 24–34 (average 29) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are broadly expanded. There are 28–31 (average 30) subdigital lamellae in males, 27–30 (average 28) in females under the second and third phalanges of the fourth toe.

Coloration. This is a mossy grey-brown anole with green or yellow-green tinges variably present dorsally, on face, limbs, and orbital area. The venter varies from pale greenish to yellowish grey. Some individuals (especially old males) have pink suffusions on the head. There are irregular dark spots and mottlings arranged in rough, forward-pointing V's across the dorsum; these are usually obscured middorsally by dark color in females. There is a vague, pale flank stripe indicated at least anteriorly; there is a bold, light bar or stripe across the forearm insertion. Chins vary from pale yellowish to grey and are usually mottled with darker grey. Both sexes have large throat fans: dull orange-yellow with virtually white to grey-green scales. Color change is merely to darker.

There is no apparent geographic variation in color, except that MCZ 82017, from the south rim of the old crater of Soufrière, at *ca.* 3000 feet was fairly dark.

Color patterns of both sexes are shown on Plate 3.

Size and sexual dimorphism. An adult male, MCZ 82926 (Kingstown), measured 136 mm fresh dead, and is 127 mm at present, snout to vent. Every male specimen examined, even including one 37 mm in the type series, has large, well-developed testes; I estimate that one like MCZ 82011 (Fancy), at 70 mm, is about as small as they actually breed. The largest female examined is 86 mm (MCZ 82015, Waterloo); the smallest with eggs is 57 mm (MCZ 82925, Colonarie River above South Rivers, *ca.* 1000 ft.). Females do not grow nearly so large as males, but are otherwise exceedingly similar in every respect of externals. Every specimen can be readily sexed by dissection.

The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

Population structure and ecology. This is a "big tree lizard": it is big, it is decidedly arboreal, and, to cap the verbal ambiguity, it prefers big trees. Human depredations on big trees in the lowlands give a somewhat clumped appearance to its otherwise infradispersed population structure. Males tend to perch from six to twenty-five feet above the ground, females occasionally come lower. It is rare to see *Anolis griseus* on the ground; in Kingstown I have seen both sexes, however, come down on the ground to eat small red berries that looked like mulberries (and may have been). Large males are so arboreal, and live on such big trees, that collecting them can be very difficult; for this reason, my size record above may well be exceeded.

Field evidence indicates a balanced sex ratio.

Distribution. Anolis griseus is common throughout the mainland of St. Vincent, but I have not seen any on the coastal cays; perhaps they are too scrubby.

Relationships. This species seems to be a direct descendant of *Anolis luciae* and must be the direct ancestor of *Anolis richardi;* its relationship to the latter form will be given more detailed consideration under that species.

Anolis richardi Duméril and Bibron

Anolis richardii Duméril and Bibron (1837: 141)
Anolis occipitalis Gray (1840: 112)
Anolis stenodactylus Gray (1840: 114)
Anolis trossulus Garman (1887: 38)

Type. MNHN Ig. 53, Richard coll: *fide* Underwood (1959).

Type locality. "Tortola"; the species does not, and never did, occur on this small island in the British Virgins. I assume this to be a blunder, and suspect the real type locality was the somewhat similar sounding Tobago. I, therefore, revise the type locality to Crown Point, Tobago, where this species is abundant.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined; sublabial scale row breaks up into undistinguished scales below eye; usually four or fewer scales of the supraorbital semicircles abut on top of head; if more, then interparietal separated from supraorbital semicircles; twelve or more (12–15) middorsals contained in ten per cent of the snout-vent length at midbody.

Squamation. One hundred nineteen specimens (71 males, 38 females, and 10 juveniles) have been examined. In addition to diagnostic characters cited above, this species differs from other Lesser Antillean *Anolis* of the *roquet* group in the following features: There are 22–31 (average 27) midventrals in the standard distance; they are tectiform to sharply carinate, and smaller than the middorsals. There are 18–23 (average 21) middorsals in the standard distance. The dorsal granules decrease abruptly in size laterally; there are 29–41 (average 35) six scale rows lateral to the dorsal midline. The digital dilations are broadly expanded; there are 23–28 (average 26) subdigital lamellae in males, 22–26 (average 24) in females, beneath the second and third phalanges of the fourth toe.

Coloration. This species varies considerably in coloration geographically, and it is a temptation to describe at least one race; however, the sum of the variation is so gradually clinal that to do so would be misleading. Four series of specimens, collected by me, are missing from the material borrowed from the MCZ. They are from localities of crucial importance in assessing geographic variation in colors, and it is fortunate that I retained all the color notes and field sketches. These are MCZ Field Tags X-17824–7, Mabuya Cay off Carriacou, Grenadines; MCZ Field Tags X-17886–93, Point Saline, Grenada; MCZ 60773–7, 60780–6, one and one-half miles north of Point Saline, Grenada; and MCZ Field Tags X-18057–66, Crown Point, Tobago. All of these 34 specimens have been added to the sum of 119 specimens noted above in considering geographic variation in color and pattern, making 153 in all.

At Crown Point, Tobago, specimens vary from uniform dark green to greenish brown in ground color. Many, especially females, have dark speckles, sometimes arranged in oblique lines. There is frequently, but not always, a light area below the eye (suboculars and sometimes supralabials). Venters are pale grey-green, often with a yellowish wash; the chin may be similar, or washed with dull yellow. The throat fan, in both sexes, is dull orange with grey-green scales. Some specimens from Crown Point will match some specimens from any locality in the range of *Anolis richardi;* there are no populations composed of distinctive individuals. Color change is always merely to darker.

There are, however, some spectacular average differences. Individuals from Bequia, the extreme northern limit of the species range, and less than six miles from St. Vincent (but nearly 140 miles from Crown Point), may be rich forest green with deep blue suffusions on the head, especially pronounced under the eye. Their chins may be brilliant yellow with blue blotches, and set off from their throat fans by an area of blue-grey; the fans may be bright orange-yellow with white scales. On the other hand, Bequia specimens may have a few speckles, or remnant dorsal chevrons; their chins may be dull yellowish; blue tones may be absent, leaving merely a light subocular area; and their fans may be dull orange with grey-green scales.

At the opposite extreme of the Grenada Bank is Point Saline. Here, *Anolis richardi* may be a dusty grey-brown with extensive white piebalding on the head and anterior body; spotting is frequently heavy: sooty dots bordered by ash grey; the orbital area may be richly suffused with yellow. On the other hand, individuals may be olive, lack piebalding, have only a few spots and those not notably bordered, and lack orbital yellow.

Certainly, if Point Saline material were compared with Bequia material in the absence of specimens from the rest of the range, there would be no doubt about a racial difference at a 90–95 per cent level. However, the entire remainder of the species range, from southwestern Grenada through the Grenadines, is a gradual, continuous cline. The brilliant blue and yellow chin hues decrease in frequency at Mabuya Cay, and are rare in northern Grenada (e. g., 81992–5, Tufton Hall). White piebalding clines from an extreme at Point Saline (e. g., MCZ 81324) to occasional patches at St. George's (e. g., MCZ 81956 or 81958). Heavy spotting occurs as far north as Petite Etang, Grenada (MCZ 81985–91), a rain forest locality. As noted, the Tobago population looks as though it came right out of the middle of this cline, and is not extreme in any respect. In sum, I cannot justify subspecific recognition of even the Point Saline population.

Color patterns of adults are shown on Plate 3.

Size and sexual dimorphism. This is the largest Lesser Antillean anole. A male from Crown Point, Tobago, measured 140 mm, snout–vent, fresh dead (MCZ Field Tag X-18057); there are a number of preserved specimens over 125 mm (e. g., MCZ 83041–2, Store Bay, Tobago). Specimens from the Grenada Bank may not grow so large; a 115-mm male (MCZ 79064), from Bequia, Grenadines, is as large as any examined. Males as small as 70 mm (MCZ 81982, Corinth, Grenada) certainly appear mature, but so does MCZ 81983, from the same locality, and it is only 59 mm. The largest female examined is 77 mm (MCZ 83044, Store Bay, Tobago); the smallest mature female is 56 mm (MCZ 81980, Sugarloaf, or Levera Island).

As in *Anolis griseus,* this species shows little sexual dimorphism in color and squamation. The standard distance is 14–17 (average 15) per cent of the snout-vent length in both sexes.

Population structure and ecology. Like its very close relative, *A. griseus,* this is a "big tree lizard" throughout its Grenada Bank range. On Grenada proper, *A. richardi* is fairly infradispersed, except where human depredations have wiped out the big trees. In the Grenadines, a highly clumped structure is imposed by the fragmentation of the land areas, and the paucity of big trees. The ultimate extreme is a place like Mabuya Cay, off Carriacou: here, there is a single big tree on an otherwise scrubby little islet; about six *A. richardi* live on that tree, but the rest of the cay supports none. Obviously, this sort of thing is highly temporary from an evolutionary point of view: that tree has a limited existence, and may not be replaced; elsewhere, other suitable trees may be growing on islands not currently supporting the lizards. A state of constant change in the location of small demes must be the rule over most of the species range.

On Tobago, *A. richardi* occurs alone, and is ubiquitous. It is remarkable to see this giant species commonly perching low on fence posts or rocks; as one drives along the coast of Tobago, the huge old males, on virtually every coconut palm at about eye level, are a very prominent feature of the landscape.

Field evidence indicates a balanced sex ratio.

Distribution. Anolis richardi is abundant all over Tobago; I have not seen specimens from, or visited, Little Tobago, but certainly expect this species occurs there. On Grenada proper, this species occurs virtually everywhere, from arid coast to the top of Mt. St. Catherine (MCZ 81969). In the Grenadines, specimens have been examined from Sugarloaf (equals Levera Island, just northeast of Grenada), Carriacou, Mabuya Cay off Carriacou, and Bequia; except for the big islands (Carriacou and Bequia) the range of this species in the Grenadines must be in a constant state of flux, as discussed above.

Relationships. *Anolis richardi* and *A. griseus* are very closely related; in fact, when collecting in Tobago, and cognizant only of color characters, I concluded that the two forms were inseparable. That view was very hard to reconcile with the spectacular distinctions so evident between Bequia and St. Vincent specimens. Bequia is dry country, but *A. richardi* from other dry areas, like Point Saline, do not look much like them, and do look very much like *A. griseus.* The whole Grenada Bank shows a strong cline in characters: the closer *A. richardi* gets to *A. griseus,* the more distinct it is. This is classical Darwinian character divergence, except that nowhere do the two species occur in sympatry. Is dichopatric character divergence possible? It certainly is, provided individuals of one species are occasionally transported into the range of the other; they do not have to survive there, or establish a population: just get there, live a short time, and die.

Let us take a specific (imaginary) example: *A. griseus* (like *A. richardi*) likes big trees, such as coconut palm, and these are readily washed out to sea; the lizards climb, and seek shelter in the crowns, at times of crisis. A coconut palm, with a male *Anolis griseus* in its crown, washes off St. Vincent, and goes ashore on Bequia. The *griseus* is now in an area where all the available territories are held by *richardi;* even if he wins a perch site and successfully courts the *richardi* females, the two forms have evolved so long in isolation (before *richardi* reached the northern Grenadines, or before those islands were above water) that the result is gametic wastage. Certainly, any characters tending to exclude *A. griseus* individuals from breeding with *A. richardi* individuals will be selected for. Note also that all one needs to work this system is single individuals; it does not matter that they constitute a propagule: any individual *griseus* in *richardi* range contributes to the selection pressure for character divergence. Probably *griseus* are rarely rafted onto *richardi* islands south of Carriacou, but fairly frequently onto Bequia; probably *richardi* are quite frequently rafted onto St. Vincent. Character divergence is strong in colors, and Gorman (1968) has found a display behavior distinction; nevertheless, the two species are still far too similar to survive together. The facts cannot be reconciled with any explanation other than character divergence, so far as I know, and it is impossible, therefore, to regard forms that display character divergence as other than full species. The transferrin (Gorman and Atkins, 1968b) and squamation distinctions between the two forms add weight to this argument.

Anolis trinitatis Reinhardt and Lütken

Anolis trinitatis Reinhardt and Lütken (1863: 269)

Anolis vincenti Garman (1887: 46)

Type. A male measuring 70 mm, snout-vent length, in the "Universitetets Museum, Copenhagen," is said to be the type (Braestrup *in* Underwood, 1959). It should be given a catalogue entry of some sort, and have a tag identifying it affixed directly to it. Braestrup's translation of Reinhardt and Lütken's original color notes clearly identifies the species.

Type locality. Trinidad. Although this species does occur in Trinidad, that island is not within its natural range; it is an introduction. In addition, it is not very common there, and may be losing ground to the likewise introduced *Anolis aeneus.* To complicate matters, the two species hybridize. In the interests of taxonomic stability, I feel it is mandatory to revise the type locality to Kingstown, St. Vincent; this is the principal town and port within the natural range of this species, and it is abundant there.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales at the level of the orbit; five or more scales of the supraorbital semicircles abut, or, if fewer, then interparietal in contact with supraorbital semicircles; 37 or more dorsals in the standard distance six scale rows lateral to the dorsal midline.

Squamation. Two hundred forty-five specimens (168 males, 70 females, and 7 juveniles) have been examined. In addition to diagnostic characters cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the ventrals are smooth; there are 22–33 (average 27) contained in the standard distance at midbody. The middorsals are about the same size as the ventrals; there are 25–34 (average 29) in the standard distance. The dorsals decrease abruptly in size laterally; there are 37–46 (average 42) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are quite ordinary; there are 23–29 (average 27) subdigital lamellae in males, 20–26 (average 24) in females, under the second and third phalanges of the fourth toe. The large number of specimens examined leaves me with the distinct impression that the number of lamellae, at least distally, increases with size or age; I have previously suggested this to be the case in other species of *Anolis* (Lazell, 1966), and the question is currently under investigation by the only sure method: raising living lizards.

An adult female *Anolis trinitatis*, MCZ 82061 (Kingstown), has the second through the eighth pairs of lamellae divided; this does not appear to result from injury, and is the only example of divided lamellae in *Anolis* known to me.

Coloration. At Kingstown, males are a bright green or blue-green shading to blue or blue-grey on the head, and to bright yellow on the mandibles and venter. The orbital area is blue to slatey blue-grey. The throat fan is butter yellow with pale bluish scales in most individuals. There is some striking variation: in some there are blue patches, and MCZ 82094 had a plain "white" (palest blue-grey) fan. Females are duller, show a vague flank stripe, and frequently have a mottled or herringbone middorsal pattern; the female throat fan is tiny and not distinctively colored.

Specimens from the extreme southeast (e. g., MCZ 82064–8, Brighton) average duller than in Kingstown.

Specimens from the extreme northwest (e. g., MCZ 82097–107, Chateaubelair Island) average yellower, and the orbital area is frequently distinguished from the ground color only by faint greyish mottling.

Specimens from the extreme northeast (e. g., MCZ Field Tags X-17692–701, Fancy; apparently missing from the MCZ collection at present, but well documented in my field catalogue) are the most striking: they show little blue, have a greenish wash on the male throat fan, and bright blue to sooty black orbits sharply set off from the ground color of the head.

Specimens from the mountainous interior (e. g., MCZ 82095–6, southeast rim old crater Soufrière, 3000 feet; or MCZ 82069–76, Colonarie River above South Rivers, 1000 feet) may lack yellow tones in the dorsal ground color, and be the darkest and bluest of all.

All of this variation is individual or the result of gradual clines; no subspecies can be recognized.

Adults are shown on Plate 3.

Size and sexual dimorphism. The largest male examined is 74 mm, snout to vent (one of MCZ 6178, Kingstown). The smallest apparently mature male is 46 mm (MCZ 81364, Rathomill). The largest female examined is 57 mm (one of MCZ 6178, Kingstown); the smallest mature female is 41 mm (MCZ 82063, Kingstown). Sexual dimorphism is striking in throat fan, strong in subdigital lamellae, and present in both size and color. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis trinitatis is ubiquitous and infradispersed everywhere within its natural range to at least 3000 feet elevation. Specimens rarely perch over ten feet above ground, but even adult males may perch on rocks or on the ground on the paramo-like heights of the Soufrière. Field observations indicate a balanced sex ratio.

Distribution. Anolis trinitatis occurs throughout St. Vincent, and on all its coastal cays, to at least 3000 feet.

This species occurs in a few areas of central, western Trinidad, where it was certainly introduced. The situation that obtains between *A. trinitatis* and its close relative *A. aeneus* has been the subject of copious publication, beginning with its original documentation by Kenny and Quesnel (1959) and continuing through the most recent of many papers by Gorman and his colleagues (see especially Gorman and Atkins, 1968a, 1968b, and works cited therein). I suggested to the other interested parties (Gorman, E. E. Williams, Underwood, Kenny, etc.) that the Trinidad situation was the result of direct introduction of *trinitatis* from southwestern St. Vincent and *aeneus* from southwestern Grenada (the Trinidad specimens are precisely like those from those areas today). At the time, my opinion was poorly regarded; it is a comfort to note that Gorman and Atkins (1968a) actually stress my precise point.

The anoles were introduced, and breadfruit saplings were surely their vehicle. Because of the drama surrounding H. M. S. *Bounty* in the years 1787–9, we tend to forget that Captain William Bligh was a man of enduring perserverance: he did go back to Tahiti, he did get more breadfruits, and he did bring them to the Royal Botanical Gardens at Kingstown, St. Vincent —just as he had been commissioned to do. And he didn't settle for that: by September, 1793, when Bligh returned to England, he had made two trips from Tahiti to St. Vincent, and delivered twice the requisite number of plants. The whole story is chronicled by Mackaness (1936).

The breadfruit plants were cultivated tenderly from cuttings to saplings before transport could be undertaken. However, by the early 1800's breadfruit had reached Grenada, and from there Trinidad and British Guiana. Today, it occurs throughout the Caribbean, even in non-British territories.

It is not remarkable that *A. trinitatis* did not become established elsewhere in the Antilles proper: at any port of entry it would meet well-adapted, exceedingly abundant, vigorous congeners. In Trinidad, however, the only native *Anolis* is the forest dwelling *A. chrysolepis planiceps* (name *fide* Vanzolini and Williams, 1970). The edificarian habitat was wide open. Each sapling was a perfect perch site for the Vincentian and Grenadian small anoles; each pot must have carried their eggs. It would seem that today *Anolis aeneus* has got the upper hand in the new territories, and *Anolis trinitatis* may ultimately survive only on the Vincentian soil from whence it came.

Relationships. This species and *A. aeneus* are very close. Hybridization certainly occurs in Trinidad, but the hybrids seem teratological (Gorman and Atkins, 1968a). *A. trinitatis* seems to be a direct derivative of the a pro-*luciae* stock, but *A. luciae* has diverged far away from it today. See Evolution, below.

Anolis aeneus Gray

Anolis aeneus Gray (1840: 114)
Anolis gentilis Garman (1887: 34)
Anolis roquet var. *cinereus* Garman (1887: 35)

Type. BMNH 1946.8.28.7. Presented by T. Bell.

Type locality. None given; here restricted to Point Saline, Grenada, where this species is abundant, and shows relatively constant characters at a populational level.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below the orbit; five or more scales of the supraorbital semicircles abut, or, if less, then interparietal in contact with supraorbitals; 36 or less dorsals in the standard distance at midbody; axilla without dark, sooty pigment.

Squamation. Three hundred five specimens (198 males, 70 females, and 17 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the midventrals are smooth; there are 22–31 (average 27) contained in the standard distance at midbody. The middorsals are virtually the same size as the midventrals; there are 21–30 (average 26) in the standard distance. The dorsals decrease gradually in size laterally; there are 25–36 (average 31) in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary; there are 21–28 (average 25) subdigital lamellae in males, 19–26 (average 23) in females, under the second and third phalanges of the fourth toe. As in *A. trinitatis,* I suspect a lamellae count increase concordant with age or size.

Coloration. This species is spectacularly variable in hues and patterns, and much of the variation is geographic. At Point Saline, Grenada, *Anolis aeneus* males are basically grey to grey-brown in ground color; many have a greenish wash. There is a dark grey peppering of spots, usually arranged in transverse bars; a distinctly metallic, bronzy sheen is prevalent within these markings. The venters are paler, dingy greyish. The throat fans vary from dull grey greenish, with similar scales, to lemon yellow with white scales. The orbital area may be bluish, but it is not in sharp contrast to the ground color. The females are grey-brown and may have a bold, dark, striped middorsal pattern, a single stripe, an obsolete pattern, or transverse bars; they lack a colorful throat fan. I have seen much Trinidad material alive, and find it indistinguishable from these; Underwood's (1959) description concurs; I have not seen Guyana (British Guiana) specimens alive, but MCZ 81283–92 (Georgetown) are precisely this anole.

Throughout the rest of the Grenada Bank, its natural home, *Anolis aeneus* varies from grey to brown to bright green, or blue and yellow; there may be spots of light, or dark, or transverse bands; throat fans may be bright or dull; the pineal may be surrounded by light, or dark, or shades between. There is so much variation that verbal description is wasteful; "typical" *Anolis aeneus* are shown on Plate 3; the geography of the variation in many features is shown in Figures 8–11. Names of the Grenada Bank Islands are given in Figure 7.

Though geographic variation here exceeds in apparent magnitude that seen in several species where good subspecies may be recognized, it is polytopic, discordant, and frequently gradually clinal. No subspecies can be usefully delimited.

Size and sexual dimorphism. The largest male examined from the Grenada Bank islands is 77 mm, snout to vent (MCZ 81805, Corinth, Grenada); I have seen larger specimens from Guyana, some in excess of 80 mm (e.g., MCZ 81283, 81285–6, Georgetown). The smallest apparently mature male is 45 mm (MCZ 81696, northernmost Tobago Cay, Grenadines). The largest female is 55 mm (MCZ 81817, Perserverance, Grenada); the smallest mature female is 39 mm (David Point, or Tonger Langue, Grenada). Sexual dimorphism, as in *Anolis trinitatis,* is striking in throat fan and notable in lamellae, coloration, and size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis aeneus is abundant, infradispersed, and ubiquitous from the ground to ten or more feet above it. A strongly clumped structure, however, is imposed on the species as a whole by the fragmentation of its range into more than fifty islands and cays (see below). In the field, the sex ratio appears balanced.

At Point Saline, Grenada, I noted on 18 June 1964 several of this species devouring "mulberries" on the ground; others were seen doing the same around the Groome residence at Calliste, on Point Saline, on the same day. As when a rich horde of insects is uncovered, male territoriality seems forgotten, both sexes, and even a number of *Anolis richardi* joined in. The berries are small, dark red, tree-borne, and altogether like ordinary mulberries in appearance; I did not taste any, as I do not like mulberries.

Distribution. This species occurs throughout the islands of the Grenada Bank (Grenadines, Grenada, and cays) wherever more than herb-stage vegetation occurs. It has been introduced, from southwestern Grenada (the Botanical Garden is south of St. George's), into Trinidad and Guyana; on the former, at least, it is common and widespread in the central, western region of the island, and is reported from the inhabited (and bread-fruited) coastal cay of Gasparee. (See *Distribution, Anolis trinitatis,* above.)

Relationships and discussion. This species, I reason, must be a direct descendant of *Anolis trinitatis* (it retains the pale axilla), and the innovator of the $2n = 34$ karyotype (Gorman and Atkins, 1968b). Thus, it is also the direct antecedent of *A. extremus* and *A. roquet.* (See *Evolution,* below.)

The Grenada bank is a submarine platform low enough so that all of its nearly fifty islands may have been united as a single land mass during the last glacial height (0–40 fathoms). Throughout this bank, on every rock and cay that has so much as a single bush, from sea level to the highest volcanic peaks—nearly 3000 feet—swarms *Anolis aeneus.* This anole, like *A. gingivinus* previously described, is ubiquitous to the extent that one must regard each land area as the range of a single local population of interbreeding individuals; the species as a whole is fragmented only by water gaps. The largest, and second southernmost, island on this bank is Grenada. At its higher elevations Grenada extends well above cloud line and has extensive rain forests; its leeward coast is in an overspill area between the high peaks, and it, therefore, is quite wet also. The land areas of the remainder of the Grenada Bank are dry: southern Grenada; Glover Island, to the south of it; and the Grenadines, which stretch northward nearly to St. Vincent, almost 70 miles away. The northernmost of the Grenadines, Bequia and Mustique, as well as the small cays in their vicinity, get some rain as overspill from St. Vincent when the wind is from just east of north; this effect is small, however. Also, Carriacou, 1300 feet high, gets some rain owing to cloud line fluctuations, but once again very little. The remaining islands, scattered and in clusters, get no more rain than the open sea; rarely, and purely by chance. The islands vary from low, sandy cays covered with a nearly impenetrable tangle of manchineel and thornbush to tall basalt spires, like Kick-'em-Jenny, which is 700 feet high and looks like a church steeple but for a few clumps of bushes on the crags.

Anolis aeneus, occurring everywhere, may have reached the small islands by founding colonies, or may have been left on them as the water level rose. Certainly, founding goes on today, for even small sand bars, of a very temporary nature, have anoles as soon as they have bushes. Given the fortuitous circumstances of gene flow between populations of this species, and the diverse ecological conditions of the land areas, considerable geographic variation is to be expected. In fact, the variation in this species is so spectacular, and

Figure 7. The Grenada Bank, giving names of islands mentioned in the text.

so discordant, that it is hard to visualize any pattern in it at all.

There is some correlation of variants and ecology: thus uniform green individuals occur only in wet forest areas (on mainland Grenada); banded individuals occur only in xeric places (southwest Grenada and some Grenadines). Beyond this, however, correlations fade. Some of the driest of the Grenadines, like Petite Tobago, have unbanded anoles; Bequia, a large, well-wooded, and fairly moist island, has anoles virtually identical to those of Kick-'em-Jenny—a dry basalt spire. The anoles of

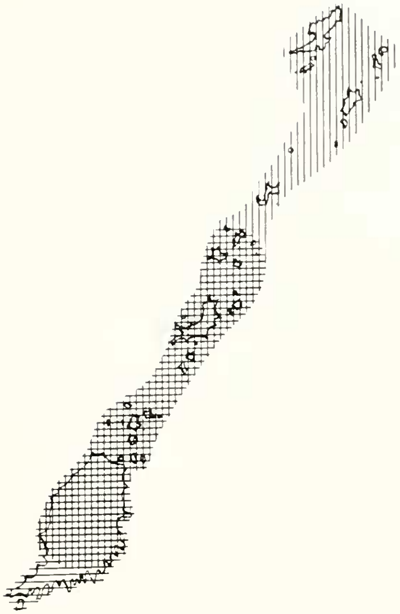

Figure 8. Variation in *Anolis aeneus:* pineal pigmentation: horizontal lines, white; vertical lines, black; intermediates may be black, white, grey, or pied.

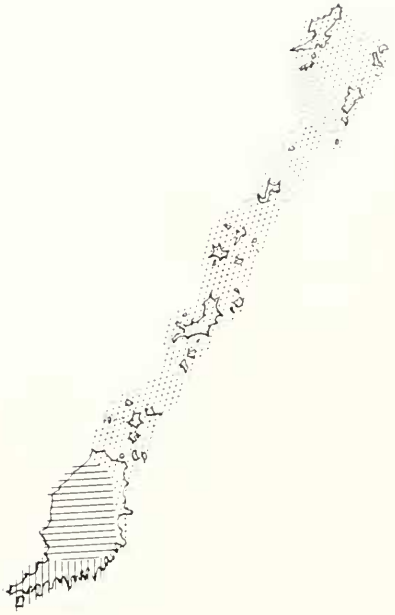

Figure 9. Variation in *Anolis aeneus*: throat fan color: horizontal lines, yellow; vertical lines, grey; dots, individual variation including combinations of grey and yellow, and olive intermediates.

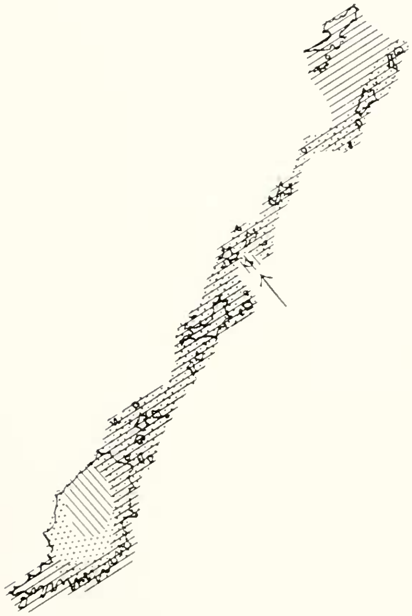

Figure 10. Variation in *Anolis aeneus:* markings on trunk: lines ascending left, uniform—no markings; dots, light speckles; lines ascending right, chevronate bands. Arrow indicates Prune Island.

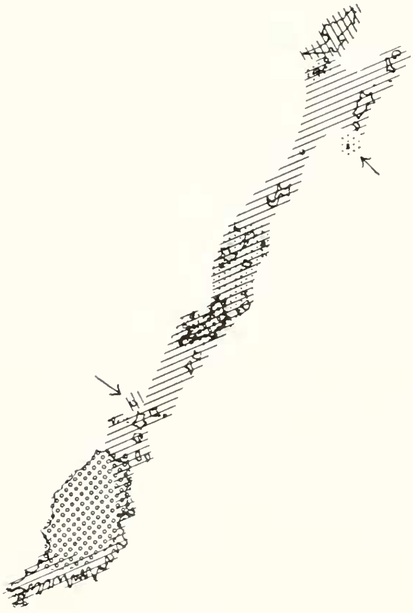

Figure 11. Variation in *Anolis aeneus:* ground color: lines ascending left, blue and yellow; dots, brown; lines ascending right, grey; open circles, green. Arrows indicate Sovan and Kick-'em-Jenny.

Glover Island are somewhat different from those of adjacent Point Salines: darker, frequently greener, and often unbanded.

When water levels were lower, the present islands of the Grenada Bank may have been parts of a continuous land area occupied by *Anolis aeneus.* Geographic variation, I speculate, was neat, even if polytopic: bright colors (green, or blue and yellow) may have characterized wet country anoles, dull colors (grey or brown) dry country animals; similarly, banding may have been characteristic of xeric areas, uniform color or light speckles of rain forest. Rising water initially fragmented this species into local populations on islands of very diverse sizes, and thus of very diverse potentialities as sources of, and landing stages for, propagules. Subsequently, rafting from one island to another (and some far more than others) resulted in the chaotic scramble of phenotypes scattered about today. At least Kick-'em-Jenny may support this theory: it was probably a lone peak intermediate between a large lowland area (sea bottom today) and a high massif (Isle-a-Ronde, Isle-a-Caille, Les Tantes group); if the lowland was dry (grey or brown anoles, heavily banded) and the massif was wet (unicolored or speckled anoles of bright color), then Kick-'em-Jenny would be expected to have intermediates: perhaps banded anoles with bright colors.

Kick-'em-Jenny has no beaches and its sheer cliffs make a heavy, pounding surf of the swells coming across the shallow Grenada Bank towards it. Very few things have ever approached it on the water and lived to land there. If Kick-'em-Jenny had, when it became an island, banded, bright colored anoles, it should have them still, uncontaminated by new colonizers; it does.

Anolis extremus Garman

Anolis roquet var. *extremus* Garman (1887: 35)

Type. MCZ 6183, Garman coll. I have affixed the tag bearing this number to the largest male, and regard it as the type; the others in this series are regarded as paratypic.

Type locality. Bridgetown, Barbados.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below the orbit; five or more scales of the supraorbital semicircles abut, or, if fewer, then interparietal in contact with supraorbitals; dorsals in standard distance 36 or less; axilla with dark, sooty pigment; head comparatively broad: width between orbits, across supraorbital semicircles at narrowest point, contained in standard distance less than four times.

Squamation. One hundred seventy-six (103 males, 39 females, and 34 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the midventrals are smooth; there are 20–29 (average 25) contained in the standard distance at midbody. The middorsals are about the same size as the ventrals: 20–28 (average 24) are contained in the standard distance. The dorsals decrease moderately in size laterally; 26–34 (average 30) are contained in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary: there are 22–28 (average 26) lamellae under the second and third phalanges of the fourth toe; although the lowest counts come from females and juveniles, there is not a significant average difference between the sexes.

Coloration. This is a mossy looking green anole; there is usually blue-grey or lavender about the head, and lichenate black or dark brown markings on the anterior trunk; there may be small, light dots. The venter is yellow; the male throat fan is orange with yellow to greenish scales. Females are more olive green and generally duller than males; they lack a colorful throat fan, and may have striped or obsolete middorsal patterns.

There is some geographic variation: specimens from Ragged Point (MCZ 81904–8) are noted as being duller than most in Bridgetown, Speightstown, or Bathsheba, and tended more towards violet tones anteriorly. One from South Point (MCZ 81909) was virtually plain grey, with only a posterior wash of green; all (MCZ 81909–13) had bluish eyelids contrasted to darker orbits. Some of MCZ 81903–4, from North Point above Animal Flower Bay, were similar. Three series from as much of an "interior" as Barbados has (MCZ 81920–24, Castle Grant Hill, 1110 feet; MCZ 81925–29, Gun Hill; and MCZ 81940–44, Mount Hillaby, 1115 feet) average a shade greener, and sometimes have more light dots than most from elsewhere.

Specimens taken by me in Castries, St. Lucia (MCZ 71822–33) were identical to typical Bridgetown specimens in life. I have not seen living material from Bermuda, but there is not the remotest doubt about the identity of the preserved specimens examined.

Adults are shown on Plate 3.

Size and sexual dimorphism. The largest male examined is 83 mm, snout to vent (MCZ 80409, "Barbados"); the smallest apparently mature male is 46 mm (MCZ 75432, Ireland Island, Bermuda); the smallest Barbados male (MCZ 75285, St. Ann's Fort) and the smallest St. Lucian male (MCZ 56390, Castries) are both 53 mm. The largest female is 60 mm (MCZ 80414, "Barbados"); the smallest mature female is 42 mm (MCZ 75296, White Hall, Barbados). Sexual dimorphism is strong in throat fan, insignificant in lamellae, weak in size, but notable in color. The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

I submit that MCZ 81903, taken by me at Bridgetown, 18 July 1964, holds the world's record as the smallest lizard ever taken with 6 pound test monofilament: 23 mm, less than .016 of an ounce.

Population structure and ecology. Anolis extremus is infradispersed, utterly ubiquitous, and exceedingly abundant all over Barbados. Thomas Barbour (1930b) notes of this species that it is "almost if not quite extinct on Barbados" (p. 112); that remark must certainly stand as one of the great verbal monuments of all time, but whether to a lizard's incredible fecundity, or a man's incredible myopia, I cannot be sure.

This species is abundant in Castries, St. Lucia; ubiquitous and infradispersed, it seems to be extending its range. I know nothing about its population structure on Bermuda, where *Anolis bimaculatus leachi* and *Anolis grahami grahami* also occur as introductions.

In the field, the sex ratio appears balanced.

Distribution. Anolis extremus is a native of Barbados, where it covers the island. It has been introduced in the recent past to Castries, St. Lucia, Bermuda, and the Centro Baleanico restaurant, Caracas, Venezuela (MCZ 110294–5).

Relationships. This species is very close to *Anolis aeneus*, on one hand, and *Anolis roquet*, on the other. It shares a transferrin with the former, a hemoglobin with the latter (Gorman and Dessauer, 1965, 1966); in display behavior it is unique (Gorman, 1968).

The axillary pigmentation makes a simple distinction between *extremus* and *aeneus*, especially when specimens (even preserved) are compared directly. Separation from *roquet* is more difficult; directly compared, *extremus* look notably broad headed; quantification is tricky, owing to the skull-covering soft tissues, the small size of the distances to be measured, and the location of the "center of the eye."

Anolis roquet (Lacépède)

Lacerta roquet Lacépède (1788)
Anolis martinicensis Suckow (1798)

Anolis cepedii Merrem (1820: 45)
Anolis goudotii Duméril and Bibron (1837: 108)
Anolis alligator Duméril and Bibron (1837: 134)

Type. None ever designated. This species is difficult to identify by conventional museum techniques, is remarkably variable, and has six subspecies that require description (below). It is imperative that a neotype be designated; that specimen is MCZ 81581, taken 29 July 1964 at Fort-de-France, Martinique (J. Lazell): an adult male 79 mm, snout-vent length.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below orbit; five or more scales of the supraorbital semicircles in contact, or, if fewer, then interparietal in contact with supraorbitals; 36 or fewer dorsals in the standard distance; axilla with dark, sooty pigment; head relatively narrow: width between orbits, across supraorbitals at narrowest point, contained in standard distance four or more times.

Remarks. Martinique and *Anolis roquet* require an introduction; Vandercook (1938) provides it:

> Martinique is steeply mountainous. Since its rainfall is nearly double that of the Leeward Islands, it is richly fertile. Fields that are level enough for the purpose are planted with bananas, coconuts, and cocoa, all of which add picturesqueness to the landscape. The many ravines and peaks that are too sheer for cultivation are covered with dense forest.

The ecological complexities of Martinique include all of the conditions I have described (see Introduction), from rain forest and rain shadow, through overspill and snags, to cays so low as to receive no more rainfall than the open sea.

Squamation. I have not found even significant average differences in squamation between the subspecies of *Anolis roquet*. I have examined 1,105 specimens (773 males, 251 females, and 81 juveniles). In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the ventrals are smooth; there are 19–27 (average 23) in the standard distance at midbody. The middorsals are virtually the same size as the ventrals: there are 19–27 (average 24) in the standard distance. The dorsals decrease gradually in size laterally; there are 25–35 (average 30) in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are broad and raised; there are 23–30 (average 27) lamellae in males, 20–27 (average 24) lamellae in females, under the second and third phalanges of the fourth toe.

A discussion of the species and its relationships follows the subspecies accounts. A table of the characters of the subspecies is given in Table 2, and their ranges are shown in Figure 12.

Anolis roquet roquet (Lacépède)

Lacerta roquet Lacépède (1788)
Anolis martinicensis Suckow (1798)
Anolis cepedii Merrem (1820: 45)
Anolis goudottii Duméril and Bibron (1837: 108)
Anolis alligator Duméril and Bibron (1837: 134)

Type. MCZ 81581, by neotypic designation (above). J. D. Lazell coll., 29 July 1964.

Type locality. Fort-de-France, Martinique, by present restriction.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color dull, mossy green to brown, usually with blue, venter dirty whitish to yellow; slate grey irregular mottling on dorsum; light dots, when present, yellow to tan; throat fan yellow to light orange, sometimes white anteriorly, with white to cream scales, and often with dark, dingy streaks between scale rows; female mossy green to brown without a distinctive throat fan; bold striped middorsal pattern; when brown, stripes sooty black; venter dirty white to yellow.

Description of the neotype. This 79 mm adult male was rich, mossy green, shading laterally to blue. The dorsum was marked by dark grey-brown mottling; small yellow dots formed oblique rows, especially on the anterior trunk. The venter was yellow. The throat fan was yellow with cream scales and dingy streaks between the scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I have examined 282 specimens of this form (187 males, 73 females, and 22 juveniles) of which 209 were collected by me. Variation is considerable, and has a geographic component. The Fort-de-France population is the standard: males are green with blue dorsally, and rarely lack oblique rows of yellow dots; their throat fans are yellow without white anteriorly. The females are green with bold dark dorsolateral stripes bordering a usually brown middorsum. The allocation of Lacépède's name is clear: no other subspecies has yellow spots. The names "*martinicensis*" Suckow and "*cepedii*" Merrem were proposed as direct replacements for *roquet;* not based on new material. The type of "*goudotii*" Duméril and Bibron (MNHN 791) is a young female typical of this subspecies. The four male syntypes of "*alligator*" Duméril and Bibron, MNHN 6791(3) and 784, are also typical of Fort-de-France material.

In the northeastern portion of the range (e. g., MCZ 82764–74 east end, Ilet Chancel), males average more heavily spotted than elsewhere, and the spots may be tan instead of yellow.

Specimens from southern coastal areas (e. g., MCZ 82239–50, Anse Gaffard; MCZ 82835–47, Rocher du Diamant; MCZ 82702–11, Ste. Luce) average browner than most, may have very bold dark markings, and may lack light spots.

Males from the Pilote valley (e. g., MCZ 82712–17, Rivière Pilote) are especially beautiful; in addition to rich green and blue, with bright yellow spots, their throat fans are usually bicolored: white anteriorly and bright, light orange with yellow scales posteriorly.

Size and sexual dimorphism. The largest specimen of *Anolis roquet roquet* examined is a male of this form, 86 mm, snout to vent (MCZ 82732, Abondance); the smallest apparently mature male is 49 mm (MCZ 66867, Anse Mitan). The largest female is 66 mm (MCZ 82132, Fort-de-France); the smallest mature female is 48 mm (MCZ 82701, Medecin). Sexual dimorphism is striking in throat fan and color, notable in lamellae and size. The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range on the mainland of Martinique; island demes are on many coastal keys, the most isolated being Rocher du Diamant: an old basalt spire that is difficult to land on, owing to a lack of beach or strand. Males perch from rocks on the ground to about ten feet up; females are usually lower, but both sexes frequently forage on the ground.

This subspecies is not especially shy or wary.

The range of *A. r. roquet* is the broad, fertile, mesic region of Martinique, and the flanking range of hills that curve down the windward coast and then west to form the southwest peninsula. This region receives considerable rain as overspill from the high mountains to the north, and the snag effects of such small peaks as Vauclin, Gardier, and Bigot.

Distribution. This is the widest ranging subspecies, covering all of central and southern Martinique, except for the extreme southeast. From Fort-de-France, the range extrends east northeast to Morne Pavillon (MCZ 82632–41), then curves northeast to the coast at Habitation Mansard-Rancée (MCZ 82815–24), and north northeast to the Ilet Chancel (MCZ 82764–74). Along the windward coast, this subspecies occurs only as far south as Le François (MCZ 82592–601); then, through the south southwest curving spine of hills it ranges to the south coast (MCZ 82732–42, Abondance; ASFS X6395, 2 km northwest of Le Marin). To the west, its range is limited only by the available land areas of the Martinique Bank. (See map, Figure 12.) This is the mesic, overspill and snag portion of Martinique.

Anolis roquet summus subsp. nov.

Type. MCZ 81630; J. D. Lazell coll., 2 August 1964.

Type locality. Poste Forestiere, Tirage 38, Deux Choux, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color bright yellow-green to plain green, without any blue; venter bright yellow-green to plain green; slate grey to sooty black irregular blotches or mottling on dorsum; light dots, when present, virtually white (very pale blue or green); throat fan deep orange with green scales; female similar or with a striped middorsal pattern boldest anteriorly; no distinctive throat fan.

Description of the type. This 70 mm adult male was brilliant green, above and below, in life. Sooty black mottling, running obliquely on the trunk, was prominent; several bright, very light blue dots were between the dark markings. The throat fan was very dark orange with bright green scales; there were vague dingy streaks between the scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I examined 125 specimens of this form (74 males, 43 females, and 8 juveniles) of which 89 were collected by me. Male variation is confined to the extent of dark markings and the size and number of light spots. Dark markings may be heavy and bold, as in the type, or reduced; they are always present. Similarly, the light spots may be large and numerous, or absent: ASFS 18879 and 18881, from 3 km southeast of Le Morne Rouge, are extreme examples, respectively; the type is about average in this respect. Females are more variable. The standard female pattern is striped, with the stripes most prominent on the neck and anterior body, and sometimes absent posteriorly. Some females, like MCZ 82851 (Morne des Roseaux) or MCZ 82162 (Petite Savane, Montagne Pelée) are indistinguishable from males in dorsal pattern; all stages of intermediacy occur: this is not a polymorphism.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 66845, Habitation Eden; the smallest apparently mature male is 49 mm (MCZ 82337, Vigie de la Calabasse, Montagne Pelée). The largest female examined is 62 mm (MCZ 82317, Habitation Eden); the smallest mature female is 48 mm (MCZ 82857, Morne des Roseaux). Sexual dimorphism is striking in throat fan, notable in lamellae, and weak in size and color. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed; from abundance at the lower elevations of its lofty range, it thins markedly past 2500 feet, and none have been collected over 3000 feet. Unlike both of the montane rain forest anoles (*A. oculatus montanus* and *A. marmoratus alliaceus*) of the *bimaculatus* group, this form is not a notable heliophile. The montane forms of the *bimaculatus* group are highly arboreal in the forest, staying close to the tree tops, and thus the sun; they are common near (or on) the ground only along watercourses, or at ponds, roads, and clearings. *A. roquet summus*, even in the deep gloom of the high forest at Morne des Roseaux, perch at about eye level, just as do their conspecifics in the rest of Martinique.

The range of *A. r. summus* is the highest mountain range in the Lesser Antilles; before agriculture cleared some areas, like the broad col between Montagne Pelée and the Morne Jacob massif, it must all have been rain forest.

This subspecies is not shy or wary, and is easily collected by noose.

Distribution. A. r. summus is found continuously through the mountains of northern Martinique from the great, smoking cone of Montagne Pelée to Absalon, above Fort-de-France. (See map, Fig. 12.) This is the montane rain forest ecological zone.

Anolis roquet majolgris subsp. nov.

Type. MCZ 81664; J. Lazell coll., 4 August 1964.

Type locality. Fond St. Jacques, north of Ste. Marie, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color dark grey-green to mud brown; venter grey to dingy yellow; dull mottling on dorsum irregular and very little darker than the ground color; whitish blotches may be present on head or anterior trunk; throat fan dull grey anteriorly, often becoming yellow or blotched with yellow posteriorly; female mud brown above, dirty greyish below; no distinctive throat fan; pattern may be striped, obsolete, mottled, or absent, but it is always dull and very little darker than the ground color; no whitish patches, or light flank stripe on posterior body.

Description of the type. This 77-mm adult male was just plain brown above and grey below; the throat fan was plain, dull grey with grey scales; faint slatey mottling was discernible dorsally. This specimen and an adult female are shown on Plate 3.

Variation. I have examined 107 specimens of this form (76 males, 27 females, and 4 juveniles), of which 52 were collected by myself. When I remarked (under the genus *Anolis*, above) that some forms were "ideally camouflaged on a dung hill," this was the one foremost in my thoughts. Males may have oblique dark mottling better indicated than in the type (e. g., MCZ 81667, from the type locality), and such marking is common at the northern end of the range (see MCZ 82134–48, Le Lorrain). A vague, grey spot or two, lighter than the ground color, appears in some from the extreme southern end of the range (see MCZ 82530–39+3, Derrière Morne). White blotches on the head, throat, nape, or shoulder are an occasional feature throughout the range (e. g., MCZ 81665, from the type locality); yellow on the posterior throat fan is common throughout the range also. Females, when they show any pattern at all (e. g., MCZ 81671, from the type locality), are very dully marked.

The name *majolgris* is my own spelling for the Creole "grey throat fan."

Intergradation with *A. r. summus*, both between the range of that form and *majolgris*, and between *summus* and the sea along the north coast, has confused many observers. Green, in *A. r. summus*, results from yellow overlying bright blue. *A. r. majolgris* virtually lacks either color; deletion of the yellow overlay signals intergradation with a coastal race in *summus*. Thus *summus* × *majolgris* intergrades may completely lack yellow (and thus green) but still retain extensive blue. A bright blue anole, in this case, is quite intermediate between a solid green one and a plain brown one.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 82520, Ste. Marie); the smallest apparently mature male is 51 mm (ASFS 18845, 4 km northwest of Ste. Marie). The largest female is 61 mm (MCZ 82537, Derrière Morne); the smallest mature female is 50 mm (82145, Le Lorrain). Sexual dimorphism is striking in throat fan, notable in lamellae, and weak in size and coloration. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range. Individuals perch about eye level, on the average, with extremes from rocks on the ground to about ten feet. Both sexes commonly forage on the ground.

The range of this species is the well-watered lowland to windward of the great barrier range of northern Martinique; it is the wettest lowland on the island.

This subspecies is not shy or wary, and is easily collected by noose.

Distribution. A. r. majolgris occurs along the northern windward coast of Martinique from Derrière Morne to Le Lorrain. (See map, Fig. 12.) This is the form of the well-watered lowland to windward of Martinique's major mountain range.

Anolis roquet zebrilus subsp. nov.

Type. MCZ 81619; J. D. Lazell coll., 1 August 1964.

Type locality. Le Carbet, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color pale grey-brown; venter dirty whitish to pale yellow; dark grey to sooty-black peppering on the dorsum, and often coalescing and combining with metallic bronze to form a chevronate pattern; whitish "frosting" on neck and anterior trunk; throat fan yellow to pale orange-yellow, usually white anteriorly, with white to cream scales, and, often, with grey streaks between the scale rows; female ashy grey-brown to olive peppered with slate grey to sooty black; no distinctive throat fan; pattern, when present, dully striped or mottled.

Description of the type. This 78-mm adult male was ashy grey in ground color; slatey peppering on the head coalesced into roughly longitudinal mottling on the nape, and sooty-black oblique streaking on the trunk. Rich bronze combined with the trunk streaking to produce four bold dorsal chevrons. The neck was frosted laterally with ashy white. The venter was pale yellow posteriorly, white anteriorly. The throat fan was light, bright yellow except for a white anterior quarter; the fan scales were virtually white. This specimen and an adult female are shown on Plate 3.

Variation. I examined 127 specimens of this form (89 males, 25 females, and 15 juveniles), of which I collected 66 myself. The general impression is of a black and white anole; there is no discernible geographic component in the variation, and all extremes may be seen at the type locality: males may completely lack the dark chevronate stripes (MCZ 81620), have dark mottling roughly longitudinally arranged on the dorsal trunk (MCZ 81622), or show pale, metallic bronze chevrons (MCZ 81621); some show great areas of white anteriorly (MCZ 81623). Females are frequently unmarked except for peppering or mottling, but may be striped (MCZ 81626), or may combine a striped middorsal pattern with the lateral components of the common male chevronate pattern.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 82418, Morne-aux-Boefs); the smallest apparently mature male is 55 mm (ASFS 18552, 5 km northwest of Case Pilote). The largest female is 63 mm (MCZ 82423, Morne-aux-Boefs); the smallest mature female is 46 mm (ASFS 18561, 5 km northwest of Case Pilote). Both of the localities cited are about in the middle of the range. Sexual dimorphism is strong in throat fan, notable in lamellae and color, but rather weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range. Individuals perch from ground level to about ten feet, averaging about eye level. Both sexes commonly forage on the ground.

The range of this subspecies is the exceedingly dry rain shadow of the great barrier range of Martinique: as arid and xeric as any area in the Lesser Antilles. This subspecies is very skittish and difficult to approach.

Distribution. A. r. zebrilus occurs along the northern leeward coast of Martinique from Case Pilote to Le Trou, south of St. Pierre. (See map, Fig. 12.) This is the arid coast to leeward of the island's principal mountain range.

Anolis roquet caracoli subsp. nov.

Type. MCZ 81601; J. D. Lazell coll., 31 July 1964.

Type locality. Pointe Caracoli, Presqu'île de la Caravelle, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color smoky grey-brown to grey-green; venter grey to dull yellow; no dark peppering; slate grey, chocolate, or sooty black transverse dorsal chevrons; tiny whitish flecks may be present, and sometimes whitish patches on neck and anterior trunk; no light flank stripe on posterior body; throat fan yellow, usually white anteriorly, with whitish scales and dark, dingy streaks between the scale rows; females smoky grey-brown without dark peppering; no distinctive throat fan; striped dorsal pattern not in strong contrast to ground color; whitish patches frequent on neck and anterior trunk; no light flank stripe on posterior body.

Description of the type. This 73 mm adult male was smoky grey-brown in ground color and had five dark chocolate chevrons on the trunk, plus two more partial ones on the tail. The venter was grey anteriorly, and shaded to dull yellow on the abdomen. The throat fan was yellow except for a white anterior quarter; the fan scales were cream; prominent, dark, dingy streaks were between the fan scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I examined 44 specimens of this form (30 males, 12 females, and 2 juveniles), of which I collected 20 myself. There is very little variation. The greenest specimen was a rather pretty lichen green: MCZ 81603, from the type locality. Some show vague mottling in the ground color (e. g., MCZ 81602, from the type locality), but this is a far cry from the peppering of *A. r. zebrilus*. Females are all smoky, and have an obscure striped middorsal pattern.

Size and sexual dimorphism. The largest male examined is 79 mm, snout to vent (ASFS X443, 3 km northeast of Tartane); the smallest apparently mature male is 54 mm (MCZ 82286, the Lighthouse). The largest female is 58 mm (MCZ 81610, Anciens Cachot, Baie du Tresor); the smallest mature female is 51 mm (MCZ 66926, Chateau Duduc). Sexual dimorphism is striking in throat fan and color, notable in lamellae, but weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. A. r. caracoli is ubiquitous and infradispersed; there are presumably demes on the tiny Ilet Lapin and Ilet Tresor, a few yards off the steep cliffs of the Presqu'île. Individuals perch from the ground to about ten feet, just as in the other subspecies. The range of this form is arid and xeric: it is so far east of the mass of Martinique as not to receive more rainfall than the open ocean.

This subspecies is wild, shy, and difficult to noose.

Distribution. A. r. caracoli occurs on the eastern end of the Presqu'île de la Caravelle. (See map, Fig. 12.) This bit of land is too far windward of Martinique's mountains to be climatically affected.

Anolis roquet salinei subsp. nov.

Type. MCZ 81675; J. D. Lazell coll., 5 August 1964.

Type locality. Pointe des Salines, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color light, bright green to ash grey-brown; venter cream to yellow; slate grey to sooty black dorsal chevrons; no dark peppering; tiny whitish flecks present, but no large whitish patches; throat fan yellow, becoming white anteriorly, with cream to white scales; no dark dingy grey streaks between fan scale rows; females ash grey-brown above, grey to yellowish below; no distinctive throat fan, striped or mottled dorsal pattern not in strong con-

Table 2. Table of the principal identifying characteristics of the subspecies of *Anolis roquet*. See text.

	Ground Color	Venter	Dark Markings	Light Markings	Throat Fan Skin	Throat Fan Streaks	Throat Fan Scales	Females
ROQUET	green to brown with blue	whitish to yellow	slate mottlings	yellow to tan dots	yellow to light orange	±	white to cream	bold stripped pattern
SUMMUS	green	green	sooty mottlings	bright whitish dots	dark orange	±	green	green belly
MAJOLGRIS	dull grey green to brown	grey to dingy yellow	vague mottlings	none (faint spots)	dull grey ±yellow	±	dull grey ±yellow	brown, vague pattern
ZEBRILUS	grey-brown	whitish to yellow	blackish peppering (sooty chevrons)	whitish "frosting"	yellow ±white	±	white to cream	peppered
CARACOLI	grey-brown to grey-green	grey to dull yellow	sooty chevrons	whitish "frosting"	yellow ±white	+	whitish	no posterior streak
SALINEI	light green to grey-brown	cream to yellow	sooty chevrons	light flank stripe	yellow ±white	–	white to cream	posterior streak

trast to ground color; no whitish patches; flank stripe indicated on posterior trunk.

Description of the type. This 72-mm adult male was pale green without blue tones dorsally, and dull yellow below. Sooty black coalesced to form four narrow chevrons across the trunk. Tiny, virtually white flecks were scattered on the dorsal trunk. The throat fan was bright yellow shading to white on the anterior quarter; the scales were cream to white in correspondence. A pale flank stripe was present on the posterior trunk. This specimen and an adult female are shown on Plate 3.

Variation. I examined 87 specimens of this subspecies (50 males, 32 females, and 5 juveniles), of which I collected 52 myself. Variation is principally in male ground color. All males taken by me at Ste. Anne (MCZ 82177–82) were very light, bright green. At all other stations individuals ranged from this hue to ash-grey. Many males lack all indication of a flank stripe. Females are all ashy, have a dorsal pattern, and a vague, light flank stripe on the posterior body.

Size and sexual dimorphism. The largest male examined was 78 mm, snout to vent (MCZ 82177, Ste. Anne); the smallest apparently mature males is 54 mm (MCZ 82192, Pointe des Salines). The largest female is 62 mm (MCZ 82183, Ste. Anne); the smallest mature female is 47 mm (MCZ

Figure 12. Martinique, showing the ranges of the six subspecies of *Anolis roquet*: 1. *A. r. roquet*. 2. *A. r. summus*. 3. *A. r. majolgris*. 4. *A. r. zebrilus*. 5. *A. r. caracoli*. 6. *A. r. salinei*.

82147, Pointe des Salines). Sexual dimorphism is striking in throat fan and color, notable in lamellae, and weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed; demes occur on the Ilet Cabrits (MCZ 81653–7), and the windward coast cays adjacent to the mainland range (e. g., 81658–63, Ilet Chevalier). As with the other forms of this species, individuals perch from the ground to about ten feet, and both sexes frequently forage on the ground.

The range of this species is so far southeast of the mass of Martinique that it receives little more rainfall than the open ocean. It is as arid and xeric as any area in the Lesser Antilles.

This subspecies is skittish, wary, and often hard to collect.

Distribution. A. r. salinei occurs in extreme southeastern Martinique from the Ilet Cabrits and 3 km southeast of Le Marin (ASFS 18678–9) northward along the windward coast to Pacquemar (MCZ

82722–31). (See map, Fig. 12.) This peninsula is southeast of the main body of Martinique. It is very low in elevation, and consequently very arid and xeric.

Discussion. As is evident from the preceding descriptions, identification of *Anolis roquet* to subspecies is very difficult except in life. The subspecies *caracoli* and *salinei* are the most difficult; I cannot distinguish between their intergrades with *roquet*, and do not really know what to call insular intergradient populations such as MCZ 82754–63, from Loup Garou.

Because of wind direction and the lay of the land, coastal cays tend to have anoles like those on the mainland southwest of them, rather than immediately adjacent. This is apparent on the Ilet St. Aubin, adjacent to the range of *majolgris:* MCZ 81611–18 combine characters of *roquet*, *majolgris*, and *caracoli*, as do those from the town of Trinité (MCZ 82540–51). This holds true all the way south to the cays off Le François, which harbor anoles combining features of *roquet* and *salinei* (e. g., MCZ 82775–84, Ilet Oscar), rather than being ordinary *roquet*, like those of the adjacent mainland (e. g., MCZ 82592–601, Le François).

It is evident from the map that a large portion of Martinique is zones of intergradation. The huge, roughly triangular area from the range of *A. r. summus* southeast to the range of *A. r. roquet* is notable: in its western, highland stretches influence from *A. r. majolgris* combines with the other two races to produce a homogeneous and rather distinctive beast (see especially MCZ 82612–21, La Duchene). I would name this as a seventh subspecies if it had any characteristics of its own; to name a three way intergrade, however recognizable and widespread, seems to me to be an inexcusable obfuscation of the real biological situation.

It has taken me six years, complete with over four months of collecting on Martinique, to finally decide to name subspecies. That naming provides the simplest and best method of describing and discussing the spectacular geographic variation in *Anolis roquet* can be challenged. Certainly, the lack of squamation differences, compounded by close convergence in the three chevronate forms (*zebrilus*, *caracoli*, and *salinei*), makes the case for parapatric subspecies far weaker than it is in either *Anolis marmoratus* or *Anolis oculatus.*

Relationships. Anolis roquet is the culminating species of its group. It shares the diploid chromosome count of 34 with both *A. aeneus* and *A. extremus* (Gorman and Atkins, 1967). It is distinct from the former in both hemoglobin and transferrin (Gorman and Dessauer, 1965, 1966) and in axillary pigmentation. It shares hemoglobin and axillary pigment with the latter. It is distinct from all in display behavior (Gorman, 1968). Further discussion is provided under Evolution, below.

EVOLUTION

> I am trying to pursue a science that is beginning to have a good many practioners but that has no name: the science of four-dimensional biology or of time and life.
>
> —G. G. Simpson (1953)

"Evolution" is a compound of many phenomena; without a fossil record of considerable depth, historical evolution—phylogeny—becomes foggy, speculative, and requires great imagination to reconstruct convincingly (even if perhaps incorrectly). Nevertheless, the garland of islands that makes up the Lesser Antilles provides a stage of incomparable quality for all of evolution's acts. *Anolis* have been players of extraordinary action: here we have at least a little of everything in the repertoire. But the curtain has been up a long time: if we believe Schuchert (1935), for about thirty million years. It is possibly fortunate, from the point of view of man's space and time, that we have missed so much: there is so much now to be seen.

Extinction. Since the passing of the Dodo, the strange, isolated animals of oceanic islands have been noted for their

PLATE 3

24. *Anolis oculatus oculatus*: male, JDL 245; female, JDL 249; Goodwill, above Roseau, Dominica.
25. *Anolis oculatus cabritensis*: male, JDL 250; female, JDL 256; Anse Gabriel, S of Colihaut, Dominica.
26. *Anolis oculatus montanus*: male, JDL 260; female, JDL 265; William Estate, Crete Palmiste, Dominica.
27. *Anolis oculatus winstoni*: male, JDL 267; female, JDL 270; Woodford Hill, Dominica.
28. *Anolis luciae*: male, MCZ 71865; female, MCZ 71690; Castries, Saint Lucia.
29. *Anolis extremus*: male, MCZ 81892; female, MCZ 81898; Bridgetown, Barbados.
30. *Anolis trinitatis*: male, MCZ 82054; female, MCZ 82062; Kingstown, Saint Vincent.
31. *Anolis aeneus*: male, MCZ 81733; barred female, MCZ 81736; striped female, MCZ 81734; all from Large Island, Grenadines.
32. *Anolis griseus*: male, MCZ 82927; female, MCZ 82932; Kingstown, Saint Vincent.
33. *Anolis richardi*: male, MCZ 81954; female, MCZ 81958; St. Georges, Grenada.
34. *Anolis roquet roquet*: male (the neotype), MCZ 81581; female, MCZ 81588; Fort-de-France, Martinique.
35. *Anolis roquet summus*: male (Type), MCZ 81630; female, MCZ 81639; Poste Forestiere, Tirage 38, Deux Choux, Martinique.
36. *Anolis roquet majolgris*: male (Type), MCZ 81664; female, MCZ 81672; Fond St. Jacques, Martinique.
37. *Anolis roquet zebrilus*: male (Type), MCZ 81619; female, MCZ 81626; Le Carbet, Martinique.
38. *Anolis roquet caracoli*: male (Type), MCZ 81601; female, MCZ 81648; Pointe Caracoli, Martinique.
39. *Anolis roquet salinei*: male (Type), MCZ 81675; female, MCZ 81648; Pointe des Salines, Martinique.

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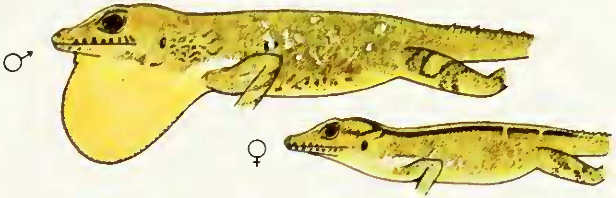

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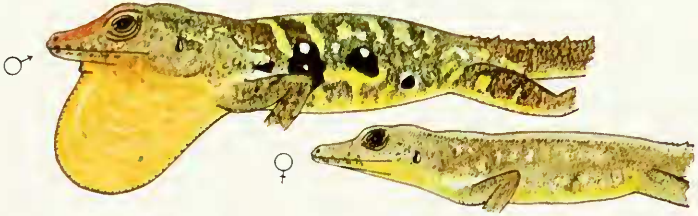

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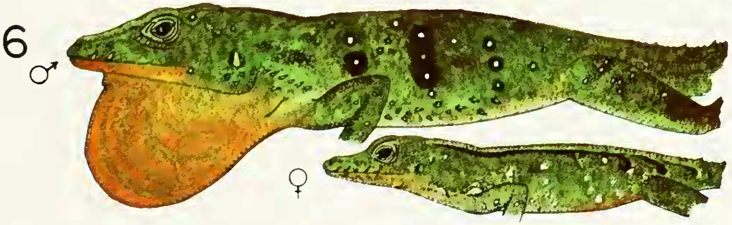

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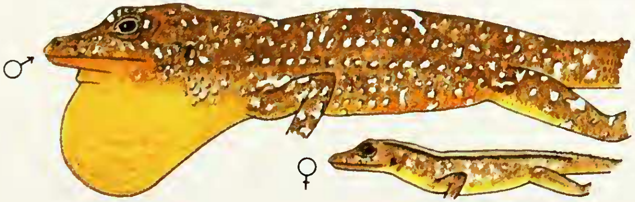

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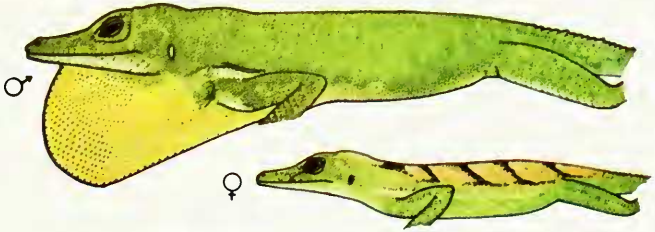

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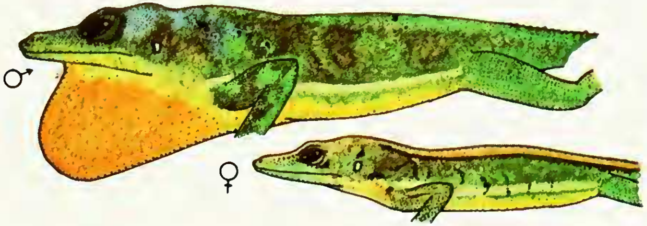

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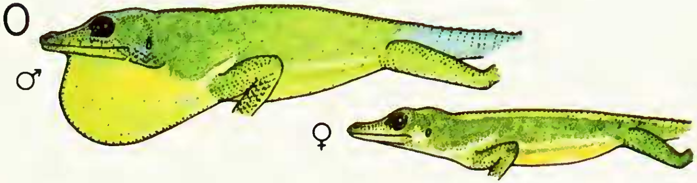

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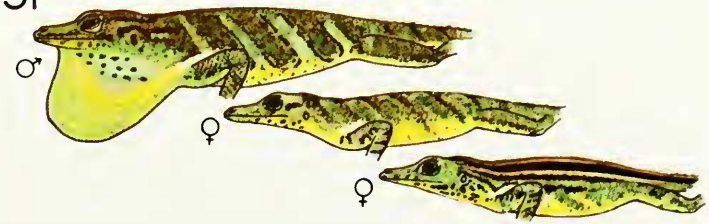

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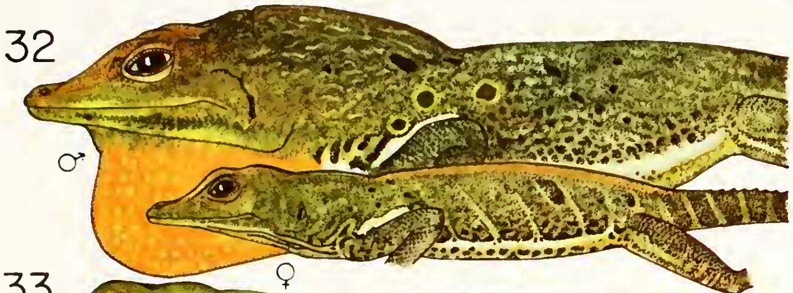

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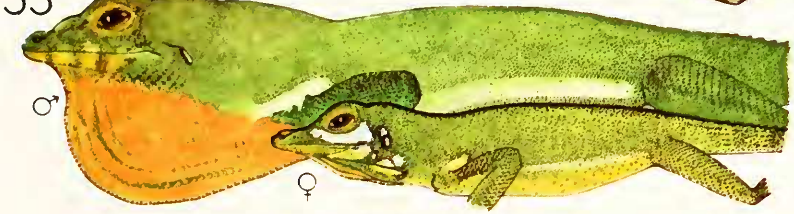

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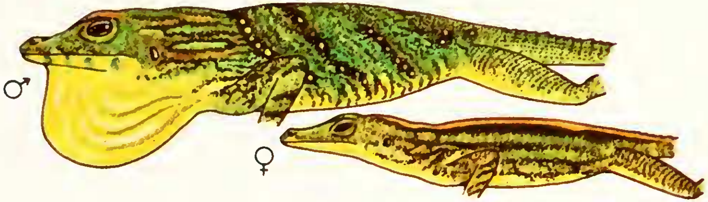

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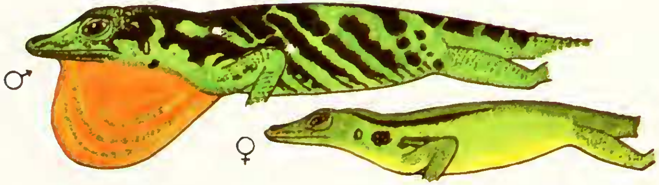

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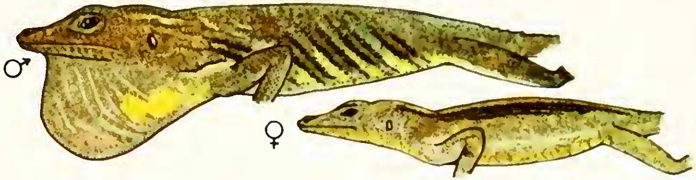

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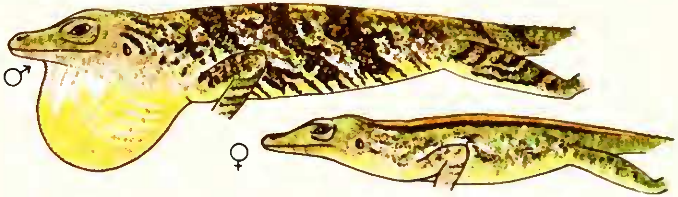

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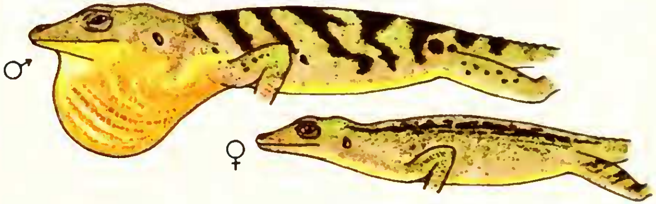

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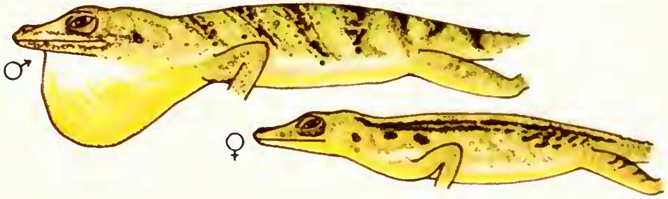

ability to become quickly extinct. It is encouraging to look at the Lesser Antillean anoles in this respect, for present evidence indicates that this is one of the major evolutionary phenomena that they have indulged in the least.

One population of a form still living seems to have been extirpated: *Anolis wattsi pogus* occurred on Anguilla as recently as 1922.

What has been the causal agent of this extirpation? Of one thing we can be sure: it has not been the infamous mongoose. Mongooses have been introduced into St. Croix, St. Martin, St. Kitts, Nevis, Antigua, La Guadeloupe and Grande Terre, Marie Galante, Martinique, St. Lucia, St. Vincent, Grenada, and Barbados. That leaves out quite a few islands, including Anguilla, from which *A. w. pogus* has vanished. Thomas Barbour (1930a, b) was the principal proponent of the theory that mongooses have wiped out lizards; aside from his classical remark on the extinction of *Anolis extremus* (1930b: 112), he also claims that both *A. griseus* and *A. trinitatis* (= *vincenti*) are "rare" and "a prey to the mongoose." Of St. Vincent he says simply, "most of the species of this Island are extinct"; with the dubious exception of one snake (two others well represented), I do not know of any species that are missing from the original Vincentian roll call. I do not wish to be misunderstood, there is no more devout deprecator of the mongoose than I: *Herpestes* is a nasty, smelly, disease-carrying, and thoroughly wretched beast; its contribution to the great faunal losses of the Antilles cannot be denied (see e. g., Lazell, 1967b). The mongoose, however, has not been significant with respect to *Anolis*.

Man, if his populations are not stabilized, will push other populations to their demise; however, it seems doubtful that even man can exterminate any form of Lesser Antillean anole before major starvation die-off decimates his own species. The Lesser Antilles are islands of little land, and man has not been kind to what there is; already the majority of the islands are thoroughly parasitic, depending utterly on the infusion of money directly from mother governments to maintain their human numbers. Such an artificial situation cannot long prevail; some day, not too distant, there will be many fewer people living in the Lesser Antilles than there are today. Considering man's established predilections, however, things will no doubt get worse before they get better.

Phylogeny. Taxonomy and evolutionary biology are frequently stated to be more art than science by critics seeking to bring these areas of interest into disrepute. As a taxonomist and evolutionary biologist, I delight in this criticism, and here embrace its basic thesis. What has preceded has been largely a recitation of empirically determined, objective facts; there have been a few speculations and hypotheses, but these have largely been expressed with the trepidation of a scientist teetering at the very brink of his factual margin. There is no relevant or important fossil record of Lesser Antillean iguanid lizards, and probably never will be. To reconstruct the evolution of the groups on an objective foundation is impossible. I shall reconstruct it, then, on a subjective basis. The result cannot be shown to be either right or wrong; one need not believe it or disbelieve it; there is no need to like it or dislike it; there is no necessity to even look at it. In what follows, I shall make abstract representations of real objects and arrange them in patterns that appeal to me. The couching of phrases in speculative terms now ends, but I practice no deception. Even as a mobile constructed out of odd bits of hospital apparatus is not medicine, so this is not science. In all respects, it is the purest of art.

In constructing the phylogenies, I shall make the assumption that each major character has originated only once. For a karyotype, for example, this seems quite likely to be true of probabilistic necessity;

for a character like the loss of ventral keeling, it is far less sure. Keeled and smooth ventrals must each have evolved many times in the history of the genus *Anolis;* my assumption of once only within the two species groups with which I deal could certainly be challenged.

The *Anolis* of the *bimaculatus* group are fascinating. In Figure 13 I present my view of their phylogeny. At stage 1, *acutus* stock, already established on St. Croix, and previously derived from the Greater Antilles, colonized the St. Kitts Bank; the $2n = 29$ (male) and $2n = 30$ (female) karyotype, with nine metacentric macrochromosomes, originated. There was no change in the condition of the ventrals (heavily keeled), and only minor shifts in trivial characters like scale size. The new karyotype was the single alteration.

At stage 2, this "pro-*wattsi*" stock colonized the little island of Saba; ventral keeling began to weaken: I postulate no other change at this stage; the karyotype remains as developed at stage 1.

At stage 3, massive emigration and colonization took place. Bypassing the already full islands of the St. Kitts Bank, and missing tiny Redonda, propagules still retaining some ventral keeling landed in Montserrat, Guadeloupe, and Dominica. The peculiar $2n = 31$ (male), $2n = 32$ (female) karyotype of *oculatus* arose subsequently on the latter island. Also at this stage, a northward invasion put anoles on the Anguilla Bank that had or developed smooth ventrals, as did *sabanus,* who stayed at home. The incipient southern species of *marmoratus* and *lividus* thus retained some ventral keeling and had unmodified ear shapes; their alterations in the process of speciation have been in trivial features like scale size, body size, and (principally) in coloration. The Saba stay-at-home, incipient *Anolis sabanus*, still resembled its stage 2 progenitor (and living *Anolis wattsi*) strikingly in size, habitat, and behavior. Its alterations were in sexual dimorphism, coloration, and, as noted, loss of ventral keeling. Incipient *gingivinus* stock was probably quite similar, exhibiting only changes from *sabanus* stock in body size, coloration, sexual dimorphism, and (very slightly) ear shape. This last feature is the beginning of a new trend.

At stage 4, *wattsi* stock invaded the Antigua Bank from the St. Kitts Bank, and Anguilla Bank "pro-*bimaculatus*" stock arrived as well: the first case of sympatry existed. With sympatry came strong selection pressures for obvious changes: body size, coloration, and ear shape diverged in the *bimaculatus* line, *sensu stricto,* and the *wattsi* stock. Also at this time, *marmoratus* stock invaded the Marie Galante Bank; changes here are trivial ones of size, scale size, and color: the form resulting is still regarded as conspecific with *marmoratus*.

The final stage 5 returned a lineage to the St. Kitts Bank as *bimaculatus* proper, and colonization of Redonda by this same stock occurred. St. Kitts Bank *wattsi* invaded the Anguilla Bank to establish sympatry with *gingivinus*. The tiny Sombrero Bank acquired *gingivinus*, and Les Iles des Saintes were colonized by *marmoratus*. If one uses degree of subsequent differentiation as a guide, that order is reversed, and Sombrero has been the last colonized; in fact, *gingivinus* may have arrived on Sombrero by human transport. None of the changes occurring at this stage involve more than body size (average), scale size, or color. Thus, *Anolis nubilus* resembles its *bimaculatus* ancestor in such basic features as ear shape, but is innovative especially in color. The other populations, similarly, are races distinguished by color or scale size (or both) or, like Sombrero *gingivinus*, not distinguished at all.

The *Anolis* of the *roquet* group are simpler (Fig. 14). The group originated as an autochthon on St. Lucia, and had undistinguished sublabial scales. At stage 1, St. Vincent was colonized, and the *griseus* stock developed some ventral keeling.

At stage 2 the primitive St. Lucian stock

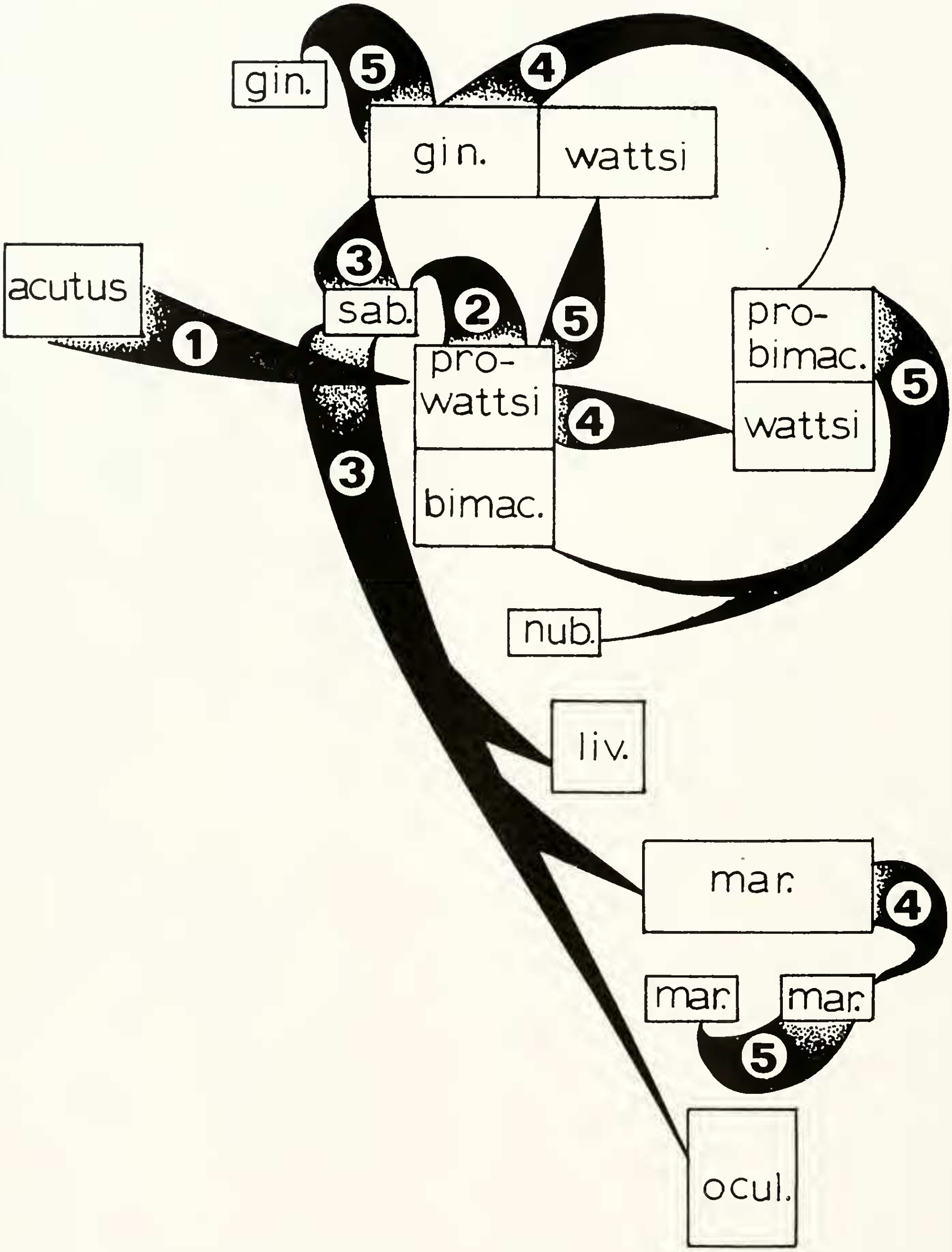

Figure 13. A hypothetical, diagrammatic scheme of the evolution and zoogeography of the species of Lesser Antillean *Anolis* of the *bimaculatus* group. Boxes represent banks; divisions within boxes represent species, not islands. Numbers indicate chronology of invasions: 1, the earliest; 5, the latest over-water colonizations; post-Colombian introductions (*A. b. leachi* to Bermuda; *A. w. wattsi* to St. Lucia) are not indicated. The same number indicates only approximate contemporaneousness: a more refined breakdown is possible. See text.

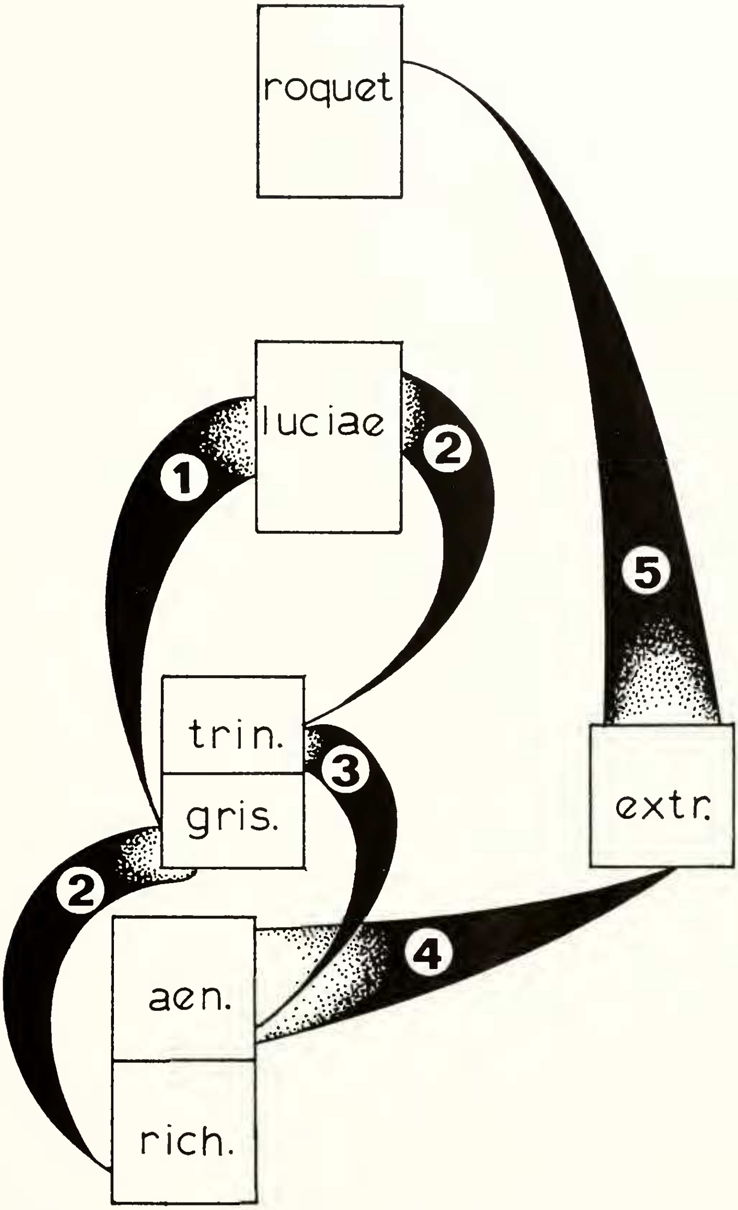

Figure 14. A hypothetical, diagrammatic scheme of the evolution of the Lesser Antillean *Anolis* of the *roquet* group; the general plan is as in Fig. 13. Extralimital colonizations (*A. luciae* stock to Bonaire and Blanquilla; *A. richardi* to Tobago) have been omitted. Post-Colombian introductions (*A. trinitatis* to Trinidad; *A. aeneus* to Trinidad and Guyana; *A. extremus* to St. Lucia) are not indicated. See text.

reinvaded St. Vincent, to give rise to *trinitatis*, a species retaining smooth ventrals. Also at this stage, *griseus* stock colonized the Grenada Bank, giving rise to *richardi*, a species continuing the trend towards ventral keeling.

Stage 3 saw a second invasion of the Grenada Bank: this time by *trinitatis* that subsequently developed the *aeneus* karyotype of $2n = 34$. The axilla remained unpigmented.

At stage 4 *aeneus* stock reached Barbados, and the resultant *extremus* developed the dark axilla. Probably at this stage, also, the *luciae* stock, with its peculiarly enlarged sublabials well in process of development, invaded far westward of the ancestral homeland: to Bonaire and Blanquilla (not shown in Fig. 14).

At stage 5 the culminating invasion of Martinique from Barbados was made, and *Anolis roquet* was born. At this or a later date (but almost certainly not by human agency), *richardi* stock reached Tobago (not shown in Fig. 14).

Except for the characters mentioned at each stage above, none of the modifications in *roquet* group evolution has involved characters other than body and scale size, and (principally) coloration. The striking distinctions between, for example, *Anolis richardi*—a giant with a short head, long legs, keeled ventrals, and little sexual dimorphism—and *Anolis aeneus*—a small form of unmodified proportions, with smooth ventrals and strong sexual dimorphism in color and throat-fan size—are attributed by me wholly to character divergence in sympatry on the Grenada Bank.

Evolutionary rates. Evolution may proceed with remarkable rapidity in populations of small size that are well isolated. Although simple, idealistic formulas for generalized biological phenomena are a commonplace today, no one seems yet to have presented such a formula for evolutionary and invasion rates. A classic example of such a simple, idealistic formula is the Hardy-Weinberg equilibrium. This is not a mathematical description of any real phenomenon, but rather an idealized formulation for a generality that never, in fact, does occur in nature: no two alleles are ever selectively neutral or equal, for example. What the formula provides is a readily calculable standard to which real gene frequencies and real frequency changes may be compared. Certainly, this is a most useful formula.

The specific question arises: What minimum number of generations is required for an allele to sweep a population, whose size is stabilized by extrinsic limiting factors (e.g., land area, food supply, etc.), given that its possessors have maximum competitive success (i.e., the rate of sweep is maximal)? I am deeply indebted to Miss P. Beth O'Sullivan, formerly a student of mine in biology, for pointing out the formula that provides the answer.

If $N =$ the number of individuals in a stable population, $X =$ the number of offspring produced per individual, and $G =$ the minimum number of generations required for an allele (appearing initially in one individual) to sweep the population, then: $X^G = N$.

$$\text{Or, solving for G:} \quad G = \frac{\log N}{\log X}$$

G may also be taken as the minimum number of generations required for an invader to establish a stable population beginning with a propagule of one (i.e., a fertilized female). In our equation, X would optimally be the maximum number of offspring per individual produced in a lifetime; using the average number of offspring produced in a lifetime tends to increase G, but is more realistic. Thus, G is either the maximum evolutionary rate or the maximum rate of territorial conquest. It is, of course, meaningful to round G up to the nearest whole number.

While there is very little empirical data on values for G, even in artificially selected populations, neither N nor X is especially difficult to determine within pragmatic limits in many natural populations. Therefore, the formula has immediate practical application as a means of accounting for both proposed rates and observed phenomena that might otherwise be difficult to explain.

For example, the population of *Anolis*

gingivinus on Sombrero might be expected to speciate at a visibly rapid rate. In fact, in applying the formula, if there are 100 *Anolis* on the island (a generous estimate), and six offspring are produced per individual in a reproductive lifetime (a low estimate), then the entire population could achieve distinction from its parental stock in only three generations. A generation (or reproductive lifetime) for these *Anolis* is probably about three years; thus, the entire population could be altered in less than a decade.

Considered from this point of view, it is perhaps not so remarkable that the tiny Ilet-à-Kahouanne, in the Guadeloupéen archipelago, has a distinct, endemic form of *Anolis*, despite its proximity and apparent ecological similarity to the mainland, and despite the fact that it has presumably been a separate island less than 10,000 years. There are surely less than 1,000 *Anolis* on this cay, and they presumably reproduce at close to the typical *Anolis* rate. Very rapid evolution is well within reason under these circumstances.

Several people have objected to this formula without, apparently, understanding it. For example, critics are proud to point out that, on the average, only one-half of an individual's offspring, in diploid organisms, will inherit the allele in question. Precisely, but that is *on the average*. The formula describes the maximal situation. It is no less likely that an anole may be the parent of six offspring, all of whom inherit the allele in question, than that a human parent may have six children, all of the same sex. As anyone living in an urban area can attest, this phenomenon occurs with dreary regularity. In any case, one may correct for this average by merely dividing X by two before proceeding.

Another, more amusing criticism is that the formula is invalid because a single allele does not make a species level difference, or even a subspecies. This criticism apparently reflects the belief that genes move through populations by some sort of osmosis, rather than by whole organisms replacing other whole organisms. The maximum speed at which one allele can sweep a population, by individuals—of course—replacing other individuals, is identical to the maximum speed an entire new karyotype and genome can sweep the population. Obviously, since the formula is the same for maximum invasion rate, it applies to whole organisms, whether they be different in one allele or a million.

It bears repeating that this formula, like the Hardy-Weinberg equilibrium, does not describe any real evolutionary event in nature. It is an ideal standard—a limit—which actually evolving populations may approach. Its value, like the value of the Hardy-Weinberg equilibrium, is that real occurrences may be compared to it, once the factual data from nature have been ascertained.

Dichopatric character divergence. When I returned from field collecting in the southern Lesser Antilles in 1964, I attempted to convince E. E. Williams, E. O. Wilson, George Gorman, and other interested persons of the reality of character divergence between presently wholly dichopatric species: *Anolis richardi* and *A. griseus*. The geographic variation in the former, as described above, cannot be explained in terms of ecology and appears to be exactly what one would expect of classical character divergence. It came as something of a surprise to me to find this phenomenon elucidated in detail by Williams (1969), especially as I had not had success in convincing anyone of the reality of the phenomenon previously. Williams, however, attributes the size difference between *Anolis marmoratus ferreus* and its neighbors to dichopatric character divergence (called by Williams, modification by "failed invasions" or "nudge effect"). This size difference, far more trivial* now that it was known to be when Williams wrote,

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* See the new size records for the other subspecies, especially nominate *marmoratus*.

is closely comparable to the size difference between St. Kitts and St. Eustatius *Anolis b. bimaculatus,* for example, and those populations are not even racially distinct. Because *Anolis* all start life small, size is a highly dubious character to employ taxonomically in this group. Its genetic basis is unknown, and it would not serve to identify any but that small percentage of the largest individuals. I have discussed gigantism in Lesser Antillean anoles under "Systematics," above, in some detail.

That *Anolis richardi,* has, though still dichopatric, diverged in characters away from *Anolis griseus,* presumably by means of selection against gametic wastage resulting from failed invasions, seems unassailable on present evidence. I am gratified that my theory has found acceptance even before its best example was described in print.

In conclusion, the taxonomy presented here is for the moment, not for all time. In ten years time *Anolis griseus* may have succeeded in invading islands of the Grenada Bank held weakly, nor not at all, by *Anolis richardi.* At present, the two species are so ecologically similar that, while invasion appears to be frequent, establishment of populations is not yet feasible. On Trinidad, two ecologically similar, previously dichopatric, forms now compete with each other (and, possibly, rare, fertile hybrids between them) for a large and desirable realm; it is too soon to tell which genotype will succeed. On St. Lucia, *Anolis extremus* is expanding despite its closely similar, if primitive, relative *Anolis luciae;* the distantly related (ecologically and morphologically) *Anolis wattsi wattsi* seems barely able to maintain a toe-hold in this land to which it was introduced by man. In the Guadeloupéen archipelago, totally occupied by *Anolis marmoratus,* races as bizarrely distinct as nominate *marmoratus* and *setosus* seem forever doomed to conspecificity by the topography of their island, while dichopatric forms as insipidly similar as *chrysops, ferreus,* and *terraealtae* proceed to speciate with respect to such a seemingly adaptively irrelevant character as the size of their scales.

Anolis wattsi pogus has transformed in forty years, before our very eyes.

The processes that make species are complex and, in the Lesser Antilles, dramatically dynamic; so are the processes that make the Lesser Antilles. These islands and their *Anolis* will repay future study, I have no doubt.

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APPENDIX: PARATYPES OF NEW FORMS

Anolis wattsi schwartzi

NEVIS: MCZ 16213–5; Charlestown: JDL* 187–92; 6 mi. E of Charlestown: MCZ 38375–6; Newcastle: JDL 198, MCZ 64339–44; Golden Rock Estate: ASFS 19563, ASFS 19542–5; White Bay: ASFS 19583–4; Nevis Peak: JDL 210–18. ST. KITTS: MCZ 28696–9; Basseterre: MCZ 75504–13; Godwin's Gut, 2.5 mi. NE Lambert's Estate Yard: JDL 168; S slope Southeast Peak, at head of West Farm Gut, 2000′: JDL 184–6; 1.2 mi. SW Lodge: ASFS 19523–5. ST. EUSTATIUS: MCZ 54708 (+ 1 untagged), MCZ 12334–6, MCZ 16538–43 (+ 1 untagged); Oranjestad: MCZ 75474–83, ASFS 19624–8; 1 mi. NE Oranjestad: ASFS X4659–61; The Quill, upper slopes at crater: ASFS 19597–615; Inside the Crater of the Quill: MCZ 75352–71, MCZ 75494–503; Behind the Mountain: MCZ 75489–93; Boven Bay: MCZ 75484–8.

Anolis wattsi pogus

ST. MARTIN: MCZ 20986; Colombier: MCZ 75798–825, JDL 101–09; Loterie: JDL 115–24; Cul-de-Sac (Dutch portion): JDL 127–36; Grand Fond, Quartier d' Orlean: JDL 152–6. ANGUILLA: MCZ 16596–7.

Anolis roquet summus

MARTINIQUE: Poste Forestiere, Tirage No. 38, Deux Choux, MCZ 81631–42; Deux Choux: MCZ 82486–92, MCZ 82858–61; Habitation Eden: MCZ 66845–7, MCZ 82311–20; Morne des Roseaux: MCZ 82848–57; Vigie de la Calabasse: MCZ 82321–37; Absalon: MCZ 82394–403; Propête: MCZ 82478–85; Montagne Pelée: MCZ 82158–66; SE slope Montagne Pelée, 2700 ft.: ASFS 18787; 5 km N Le Morne Rouge: ASFS 18577; 3 km N Le Morne Rouge: ASFS 18581; 3 km SE Le Morne Rouge: ASFS X466–9; 7 km SE Fond St. Denis: ASFS 18540; 3 km SE Le Morne Rouge: ASFS 18878–98; 4 km S Colson: ASFS 18875–7; 1 km S Colson: ASFS 18878; 4 km SW Ajoupa-Bouillon: ASFS X6621, ASFS 18728.

Anolis roquet majolgris

MARTINIQUE: Fond St. Jacques: MCZ

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* All JDL specimens are now in the MCZ.

81665–74; Derrière Morne: MCZ 82530–9 (+ 3 untagged); Le Lorrain: MCZ 82134–48; 1 km E Le Lorrain: ASFS 18827–30; 3 km SE Le Lorrain: ASFS X6483–92; Ste. Marie: MCZ 82518–29; 4 km N Ste. Marie: ASFS X425–8; 2 km SE Ste. Marie: ASFS X6454–7; 4 km NW Ste. Marie: ASFS 18831; Marigot: MCZ 82505–17.

Anolis roquet zebrilus

MARTINIQUE: Le Carbet: MCZ 81620–29, MCZ 82167–76; Case-Pilote: MCZ 82404–15; 1 km NW Case-Pilote: ASFS 18504–15; 5 km NW Case-Pilote: ASFS X454–61, ASFS 18541–64; Fond Capot: MCZ 66848–55, MCZ 82382–93; Le Trou: MCZ 82427–36; Morne-aux-Boeufs: MCZ 82417–26; 3 km SW Morne Vert: ASFS 18669–71; 2 km S St. Pierre: ASFS 18662–4.

Anolis roquet caracoli

MARTINIQUE: Pointe Caracoli: MCZ 81602–7; Anciens Cachots, Baie du Tresor: MCZ 81608–10; Lighthouse, Presqu'île de la Caravelle: MCZ 82280–9; Chateau Dubuc: MCZ 66924–6; 3 km NE Tartane: ASFS 18767–81, ASFS 1816–7, ASFS X443–7.

Anolis roquet salinei

MARTINIQUE: Pointe des Salines: MCZ 81643–52, MCZ 82187–96; Grande Anse des Salines: ASFS X6396–7; Ste. Anne: MCZ 82177–86; 1/2 km SE Ste. Anne: ASFS 18675–6, ASFS 18680–7; 1 km NE Ste. Anne: ASFS 18688–702; 1/2 km N Ste. Anne: ASFS X448–53; 3 km SE Le Marin: ASFS 18678–9; Pacquemar: MCZ 82722–31. ILET CHEVALIER: MCZ 81658–63. ILET CABRITS: 81653–7.

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